# ON SOME ASPECTS OF THE BIOLOGY, THERMAL RELATIONS, AND THERMOPHYSIOLOGY OF *LEIOLOPISMA LINEOOCELLATUM*

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The green-backed skink, Leiolopisma lineoocellatum

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# GENERAL INTRODUCTION

In recent years, the thermal relations and the thermophysiological responses for representatives of the lizard families Agamidae, Varanidae, Iguanidae, Anguidae, and Scincidae have been studied. Substantial field and laboratory observations have established that although lizards are ectothermic, they behaviourally adjust and maintain their body temperatures ($T_B$), under favourable macroclimatological conditions, within a certain range. The ranges of 'optimal' or 'preferred' $T_B$ vary interspecifically even in the same environment. The physiological significance of these preferred $T_B$ has received considerable study only in the last decade. Most of the attention has been directed toward their physiological performance at non-injurious $T_B$ (particularly high $T_B$) and heat resistance. There is a paucity of literature on the physiological responses of lizards to low $T_B$.

The thermoecology and physiology of New Zealand lizards have not been studied. Work on congeneric species is also limited. Most of New Zealand's lizard species are viviparous. Viviparous lizards do not appear to be limited in latitudinal distribution but are excluded from extreme environments of polar and desert regions. Oviparous species, however, are restricted from cooler regions where individuals can exist but where successful breeding and development cannot occur.

The underlying objective of this study was to test the hypothesis that New Zealand lizards are physiologically adapted* to be active at low $T_B$. For this purpose, a single species was chosen and the scope was limited to intact animals with the emphasis on relating and comparing data with other work on lizards.

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* 'Physiological adaptation' refers to any physiological property or response of an organism which favours survival in a specific or changed milieu, particularly a stressful one, and which is relatively long term and genetically determined. Such an adaptation provides the basis for natural selection and speciation (Prosser, 1961).

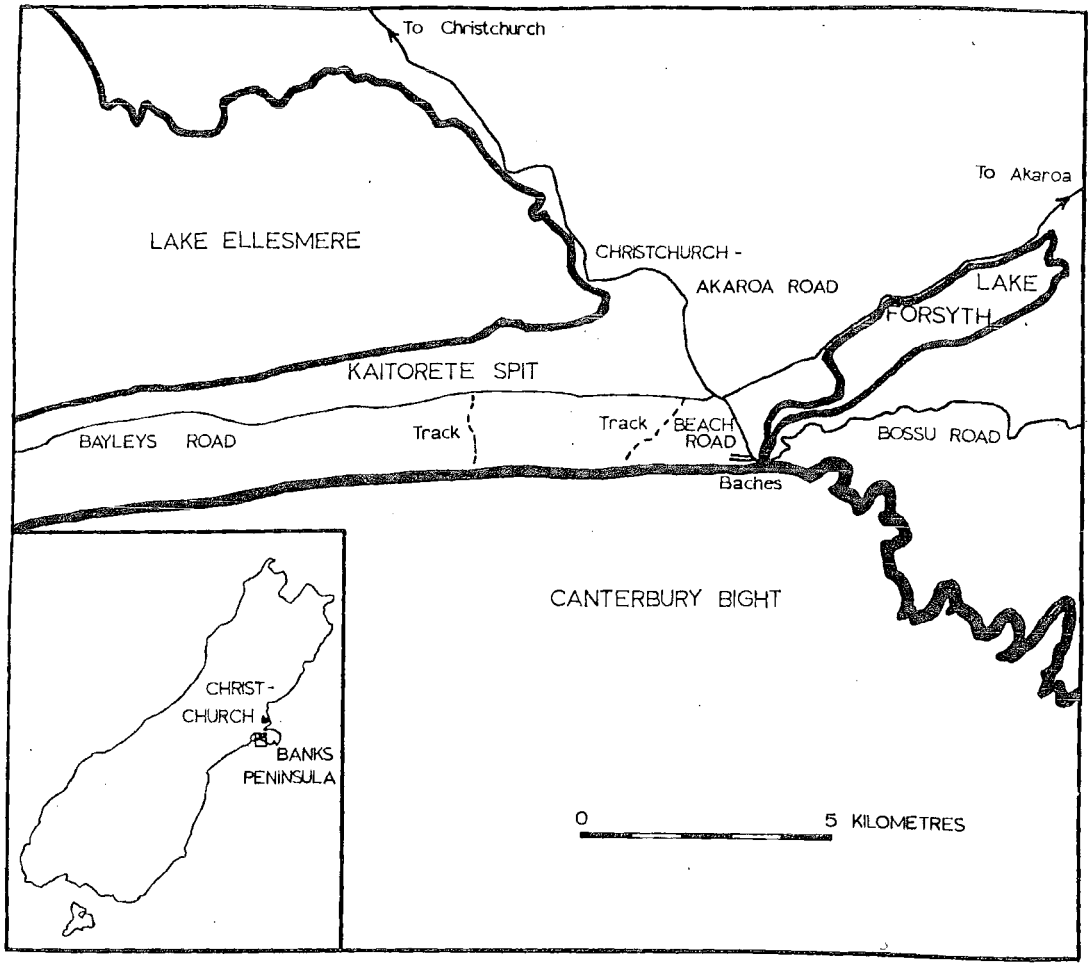
To Christchurch
To Akaroa
LAKE ELLESMERE
CHRISTCHURCH -
AKAROA ROAD
LAKE
FORSYTH
KAITORETE SPIT
BAYLEYS ROAD
Track
Track
BEACH
ROAD
BOSSU ROAD
Baches
CANTERBURY BIGHT
CHRIST-
CHURCH
BANKS
PENINSULA
0
5 KILOMETRES

FIGURE 1

Location of Study Area. It was a strip above the high tide line about fifty metres wide and running from the baches near Beach Road west for about ten kilometres. The Study Area was almost directly south of Christchurch.

Metabolic, ventilation, and cardiac responses were determined over a wide range of $T_B$. The rate-temperature responses of physiological processes reflect the extent of thermolability and physiological adaptation of an organism to temperature.

## MATERIALS AND METHODS

My initial unfamiliarity with New Zealand and its endemic lizard species as well as the paucity of literature on its saurians necessitated substantial groundwork before commencing a thermobiological study of a New Zealand lizard. The preliminary objectives were to locate a local habitat where lizards were available in relatively large numbers, to determine the best way to catch and keep them, and to select a suitable subject (species) for investigation.

### A. DESCRIPTION

#### 1. Study Area

Of the several locations searched locally, the Kaitorete Spit provided the best collecting area, and an interesting and not too complicated thermoenvironment to characterize.

The Kaitorete Spit is a narrow strip of land running east-west for about eighteen kilometres, bordered by the Canterbury Bight and Lake Ellesmere (Figure 1). The south-north profile is characterized by a steep shingle beach, young dunes, and a flat of older shingle extending to the lake. The beach and sand dunes vary from about one hundred to several hundred metres. Most of the width of the spit consists of a series of terraces sparsely covered with grasses, shrubs, and scramblers, and grazed by sheep.

Although lizards occupy most of the spit, the habitat from which all the study animals were obtained was a strip about fifty metres wide bordered by the beach and the sand dunes. Access to this area

was from Beach Road and the two tracks. The study area ran west from the baches for about eight kilometres. Beyond this area, cover (debris) was limited and black-backed gulls (Larus dominicanus), a a possible predator, were abundant. The dominant and almost exclus-eive vegetation was pingao (Desmoschoenus spiralis) whose rhizomes, deep roots, and hardy aerial structures are well adapted to colonize the unstable sand and to survive the stresses of salt spray, wind, and low soil moisture. Besides the vegetation and the sand-greywacke substrate, the other conspicuous components of this habitat were driftwood and other debris. Pilgrim (1969) has described this habitat in more detail. The presence of the driftwood and the fact that it changed in quantity and distribution between visits to the spit suggest that the study area is in the splash zone and within reach of the highest spring tides. The lizards which occupied this occasionally precarious habitat were probably from the adjacent dunes or flats.

The three lizard species which were captured in the study area were characteristically concealed under the driftwood or debris, or in the vegetation. The usual difficulty encountered in catching these small, active lizards by hand was minimized in this habitat by the exposed, loose sand areas between tussocks of pingao and piles of debris which prevented easy escape. The distribution of lizard species appeared to vary with the type and amount of cover. The common skink, Leiolopisma zelandica (Gray, 1843), is the most prominent and ubiquitous species. The gecko, Hoplodactylus pacificus (Gray, 1842) is less abundant and usually found under piles of debris throughout the area. The so-called green-backed skink, Leiolopisma ~~lineocellatum~~ (A. Dumeril, 1851), the largest and least common species represented in the study area, is found under debris near the baches and under driftwood or in rotten logs in the stretch -roughly between the two tracks- which appeared to coincide with the occurrence of the larvae of the sand scarab (Pericoptus truncatus) under driftwood (pers. obs.).

Unlike the flora, the fauna at the spit was conspicuously varies In the search for lizards, several other vertebrates were found. They

were similarly concealed in vegetation and under debris, and included the house mouse (Mus musculus), rabbits (Oryctolagus cuniculus), black-backed gull chicks (Larus dominicanus), and hares (Lepus europaeus). Although there was a striking variety and large numbers of invertebrate species, it is not known which species were potential prey for the large lizard population which was evident on the spit on favourable days* throughout the year. In addition to the scarab larvae, there were spiders (including the katipo, Latrodectus katipo), native earwigs (Anisolabis littorea), a native silverfish (Heterolepisma zelandica), wood lice (Isopoda), and a large variety of dipterans. The invertebrate ecology of this and adjoining areas of the Canterbury Bight have been discussed recently (Pilgrim, 1969). The large size of the fat bodies of freshly captured lizards from the study area suggests that food was not limiting and that their nutritional status was excellent. Mite infestation, common in many other New Zealand populations (Whitaker, pers. comm.), was not in evidence on any lizard captured on the spit.

2. Study Animal

Although lizards are the most ubiquitous and numerous endemic terrestrial vertebrate in New Zealand, little is known about their ecology or physiology. Only two families are represented, Scincidae and Gekkonidae. The taxonomic status of several of the species is doubtful and the generic affinities with other Oceanic lizards have not been determined, but these difficulties do not affect this study.

Of the three species present on the spit, L. lineoocellatum was chosen as the subject for study. Skinks are considerably more alert and celeritous than geckos, and yet with experience are not difficult to handle. Furthermore, skinks are less prone to caudal autotomy. L. lineoocellatum is three or more times as large as L. zelandica, making it a more suitable subject even though it was

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* In this thesis, this expression refers to days free from precipitation and with some sunshine, i.e. days of fine or fair weather.

much harder to find.

Scincids, compared to other families of lizards, are remarkably uniform in body form and have relatively limited modes of life. They comprise the largest and most cosmopolitan family of lizards but, because of their relatively small size and secretive habits, most are inconspicuous even when they occur in high densities. Many scincids live on the ground under rocks and vegetation, and a large number are burrowers. They are typically streamlined with a relatively small head, indistinct neck, long body, short limbs and smooth, shiny, imbricating scales. L. lineoocellatum is a typical representative of the family (see frontispiece).

Leiolopisma is the largest genus of skinks and is cosmopolitan. Leiolopismids occur at high latitudes (except in North America where all scincids are oviparous) and on many high mountains. Viviparity is common for those species which inhabit the cool regions of the North and South Temperate Zones and on high mountains. There is very little literature on the thermal relations of Leiolopisma species and apparently nothing on their physiological responses to temperature.

a. General Ecology

So little has been written about these skinks that is is expedient that some basic information be made available. This account is not exhaustive in its treatment but includes only pertinent and personal observations made during the preliminary phase of this study.

L. lineoocellatum is known to occur throughout the South Island except on the west coast. L. festivum, which is apparently indistinguishable from L. lineoocellatum, occurs on the North Island as far north as 38 $^{o}$S latitude (Whitaker, pers. comm.). It occurs from sea level to over 1200 metres (Mt. Mundy at 42 $^{o}$S, Whitaker, pers. comm.). There is no evidence that this species nor any other

N. Z. lizard species brumates*. Leiolopisma species are known to be active on favourable days even during the winter. L. lineoocellatum is viviparous as are most N. Z. lizards (except L. suteri which is oviparous), with perhaps two or three young being born in the period January to March. Details regarding their breeding ecology are lacking because a preponderance of males and no young were captured in the study area. This would suggest that the area was a marginal habitat invaded by the more vagile members of the population occupying the flats.

There were several potential predator species including the black-backed (Larus dominicanus), red-billed (L. novaehollandiae), and black-billed (L. bulleri) gulls, magpies (Gymnorhina hypoleuca), harrier (Circus approximans), kingfisher (Halycon sancta), and possibly rats and feral cats although none were seen in the area. Fitzgerald (1964) reported that skink remains formed about 6.5% by volume of stoat (Mustela erminea) droppings collected at Birdlings Flat (east end of Kaitorete Spit).

Although a large variety of invertebrate species were seen in the field, the only definite observation concerning the feeding of L. lineoocellatum occurred when a skink, upon capture, disgorged two empty skins of the scarab larvae. This observation, made in the winter (August 25, 1970), is particularly interesting because both the predator and its prey often occur under the same driftwood. The larvae are large, common, and slow moving suggesting that they are not only readily accessible but also easy prey. To what extent these larvae are utilized as a food source is not known. Because of the disparity in the sizes of the two diurnal skink species in the study area, they probably prey on different sized invertebrates.

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* Mayhew (1965) coined the term to include winter dormancy in ectothermic vertebrates involving physiological changes which are independent of the temperature. 'Hibernate' is reserved for endotherms which allow their $T_B$ to fall near to the $T_A$, i.e. undergo voluntary hypothermia which is unlike the imposed torpidity of ectotherms.

Skinks shed their skin piecemeal. The frequency of ecdysis is directly related to general nutrition and growth occurring irregularly during the year from every few weeks in the summer to once in a few months in the winter. Since food and water were ad libitum and the skinks were at room temperature during these observations, with only the photoperiod varying according to the season, the reduced appetite (anorexia) and reduced rate of ecdysis may be due to the shortened photoperiod in winter. The colour of the dorsal surface of L. lineoocellatum varied from 'green' immediately after sloughing to 'bronze' just before moulting. No green or blue pigments are known to occur in Squamata. The 'green' is a "structural colour" which is due to the reflectivity of the iridiocytes (containing guanine) in combination with melanin and a superficial layer of yellow lipophores acting as a filter (Bellairs, 1969). By microscopy, using strong illumination, the effect of epidermal buildup prior to sloughing can be observed. The epidermis acts as a filter to all but the yellow to red wavelengths, hence the bronze colour. It is unlikely that this colour change affects the absorptivity of the integument to long wave infrared radiation.

The sexes are very difficult to determine by external examination except during breeding season when hemipenes are visible inside the flap covering the opening of the cloaca in adult males. Although copulatory activity was not observed, sperm were present in the testes in all seasons. The hemipenes were easily stimulated to become engorged only from October to December which is probably coincident with the copulation period.

Both sexes have large inguinal fat bodies. The males have them throughout the year, suggesting that these fat reserves are not mobilized and that food is not limiting at the spit even during the winter. The size of fat bodies in pregnant females diminished during the spring and summer and remained small until the ovarian yolks had developed fully (March and April). By May, however, females also had large fat bodies. The practice of laying down

yolks before winter is a common occurrence in viviparous lizards since it permits early fertilization and development before the availability of abundant food (Bellairs, 1969).

Caudal autotomy occurred with difficulty in these skinks, and only when the tail was pulled or held firmly during escape. Geckos, on the other hand, may drop their tails even when held by the body. Autotomy in lizards is known to occur only along fracture planes of vertebrae and appears to be due to rapid contractions of segmental blocks of muscles. Vasoconstriction of the caudal artery prevents excessive bleeding. A callus is formed over the wound. A skink which had dropped its tail upon capture in March did not begin regenerating its tail until October although food was available ad libitum during the entire period. Tail regeneration probably occurs only during the spring-fall period coincident with active feeding. The annual snout-vent length (SVL) growth increment of this skink was lower than comparable-sized skinks which had intact tails. Since most skinks collected had regenerated ~~some~~ at least a small part of their tail, it would be difficult to age them strictly on the basis of their SVL. The regenerated tail never grows to the original length; it is supported by a cartilaginous rod, and has a scale pattern which is different from that of the tail stump. The tail appears to be more a distraction to predators than an aid to locomotion. The loss of the tail does not appear to affect their rate of movement. The tail is also used for fat storage since the tails of starved skinks developed a lateral flattening whereas well fed skinks (kept at room temperature with food ad libitum) had heavier, less tapered tails. Caudal autotomy is metabolically expensive considering that the tails represent up to 30% of the total body mass and contain fat reserves. The slower growing species of lizards (which includes the scincids) appear to be less prone to autotomy suggesting that autotomy may have been selected against as an escape mechanism. These species probably rely on rapid locomotion rather than on autotomy to escape from predators.

b. Behaviour

L. lineoocellatum is insectivorous and largely diurnal in habit. Its rapid movement in water or on sand is undulatory with the hind limbs pressed against its body and the front limbs used for changing direction. For slow locomotion on level or broken ground, all limbs are used and the ventral surface is held above the substrate (especially when the latter is hot). This skink is also adept at burrowing in sand as a means of evading capture and avoiding thermal stress. Its long flexible streamlined body and movable eyelid with a transparent window (palpebral disc) are considered to be adaptations for burrowing. Swimming and lying in water - although never observed in the field - occurred in the laboratory and in the terrarium. On rainy days in the terrarium, the skinks were usually found under several centimetres of wet sand or even under the water trough (which was surrounded by water) rather than in the shelter. Diving was observed on several occasions in the terrarium when attempts were made to catch the skinks resting near the water trough. When submerged vegetation or rocks were present, the skinks often concealed themselves under it. Unfortunately the short supply of test subjects prevented a determination of the nature of this response as an escape mechanism or the length of time they would have remained submerged before voluntarily resurfacing. Lizards characteristically swim well even though none of them are aquatic per se or possess any special swimming adaptations. The N. Z. skink, L. suteri, swims and dives in the field, and is known to feed in water. Whitaker (1968) reported that this nocturnal skink swims well on or below the surface of water. When disturbed, it dives into the nearest pool, staying submerged about two minutes (and as long as 3 minutes, 36 seconds) sometimes with their eyes open following movements above the surface, and periodically expelling air. On resurfacing, they were observed to ventilate rapidly and deeply. They were able to swim at least as far as eight feet under water and also to dive to at least three feet. The

Australian skink Sphenomorphus quoyii is reported to always live near water and to escape into it, although it is not known whether it also feeds in the water (Frauca, 1966).

Skinks are known to attack and engorge prey at least as large as their heads even though they have relatively small mouths. They accomplish this action by streptostyly (made possible by movable quadrates) and kinesis (assisted by a joint between the pterygoids and the braincase) which widen the gape and shift prey to the back of the mouth whence it can be swallowed (Bellairs, 1969). These actions are aided by inertial feeding during which the prey is static while the jaws are shifted over it in a series of rapid forward motions of the jaws and head. Drinking was also observed in the laboratory on numerous occasions. The water was lapped up. When water was not available in the terrarium, suggesting the problem of desiccation, mortality increased. Since fresh water sources are rare in the study area, it is possible that the skinks obtain water by licking dew off the vegetation.

No fighting, displaying of threat or other postures, or territorial behaviour were observed intra- or interspecifically in the field or in the terrarium. When prodded with a seeker some skinks seized it and twisted their bodies like a corkscrew. This motion was seen when they were tackling large prey. Although the skinks did not appear to aggregate in the field, they did so in the terrarium even when similar cover was unoccupied. They tended to be arranged side by side stretched out or coiled together.

It was found that when the skinks were placed on their backs and held by the head and the end of the tail until they were quiescent, then released, they would remain there for several minutes although their eyes were open and appeared to follow a moving hand. A loud sound or slight touch activated them to right themselves. Although this response is well known to occur in lizards, the explanation is not clear. It appears as though the lack of proprioception, or of tactile and pressure responses from the limbs and ventral surface may

have temporarily confused their central nervous system, since the skinks will not have encountered the unusual situation of sensory input from only the dorsal surface in the field. It is clear that to test the righting response of these skins at low temperatures, they must be turned over with a minimum of handling to prevent this unusual response from being mistaken as an indication of immobilization at low temperatures.

c. Capture and Maintenance

Lizards are usually captured by hand or in pit traps. The latter method is often used for capture-recapture studies or when the habitat and the traps can be checked frequently. Because only infrequent daily visits were possible in the present study and because of the relatively low density of L. lineoocellatum, it was more practicable to catch them by hand. But on hot days this was particularly difficult because of their amazing speed.

Thirty skinks were captured from the spit during the study period. They ranged from 3.4 - 13.6 grams (average, 8.6 grams) with SVL from 59 - 87 mm. All skinks captured were given a number (S.1 - S.30) and toe clipped. Although these lizards are pentadactyl, only the last four digits were used because of the small size of the first digit. No more than two toes were amputated and often fewer because of the incidence of naturally lost toes. By always removing the entire toe, it was possible to differentiate between clipped and naturally lost toes. A callus formed after clipping that was not unlike the callus which formed on a tail stump. No infection occurred.

Based on unpublished data (Whitaker, pers. comm.), the ages of the subjects were estimated to range from about 2 - 6 years of age. Those captured before the experimental phase of this study were kept in a glass-fronted terrarium at the normal photoperiod of the season (regulated by a timer) and at room temperature (15 - 23 $^{o}$C). The light source consisted of a Vita-lite lamp (Duro-Test Corporation) and, according to the manufacturers, it emitted all the wavelengths of sunlight at about the same relative energy levels as sunlight.

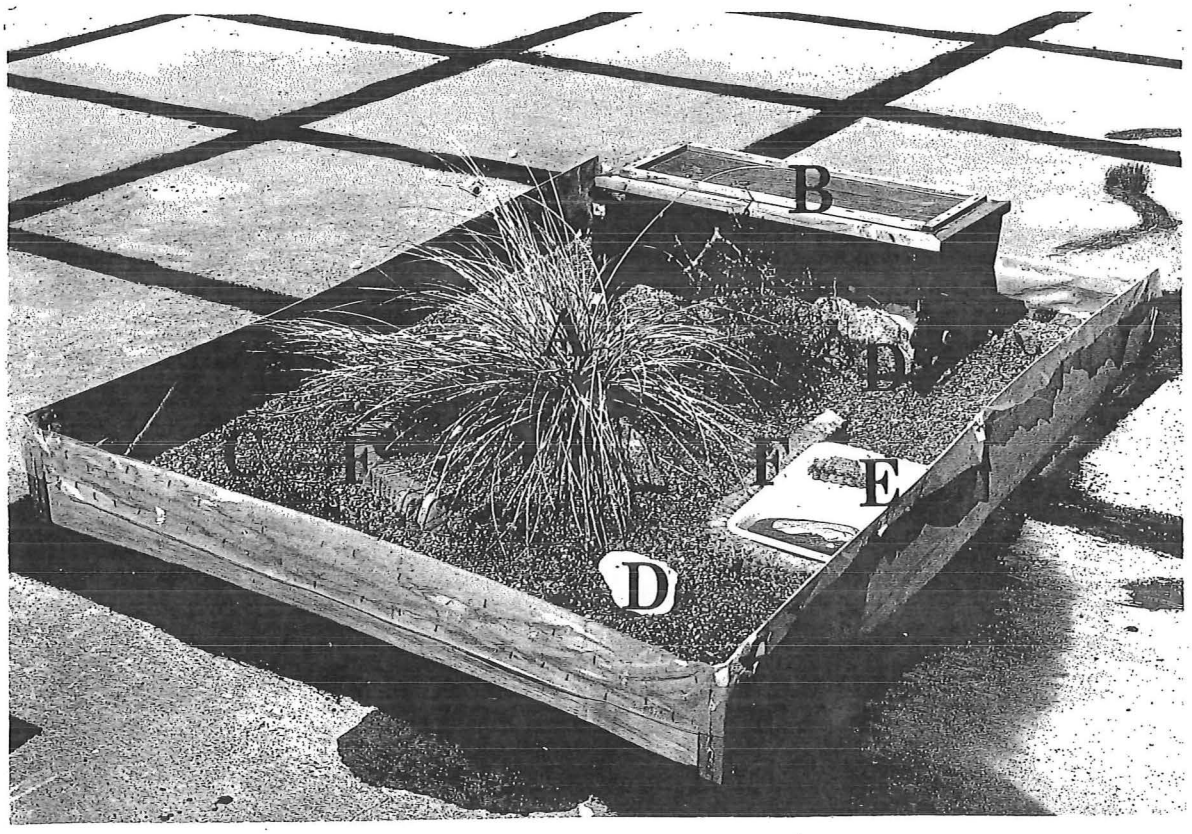
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FIGURE 2

Outdoor terrarium looking approximately from the north.
Contents of the terrarium shown are:

A. A tussock of pingao.

B. A shelter containing food station.

C. Spit sand and shingle.

D. D. Rocks

E. Water trough.

F. F. Foam rubber.

Tenebrio larvae, young Periplaneta, and water were always available. Body weights were taken fortnightly to determine the skinks nutritional status. The health and vigor of these skinks kept throughout the winter were excellent. They appeared fatter (particularly in their limbs and tails) in the spring than specimens freshly captured from the study area which had over-wintered in the field.

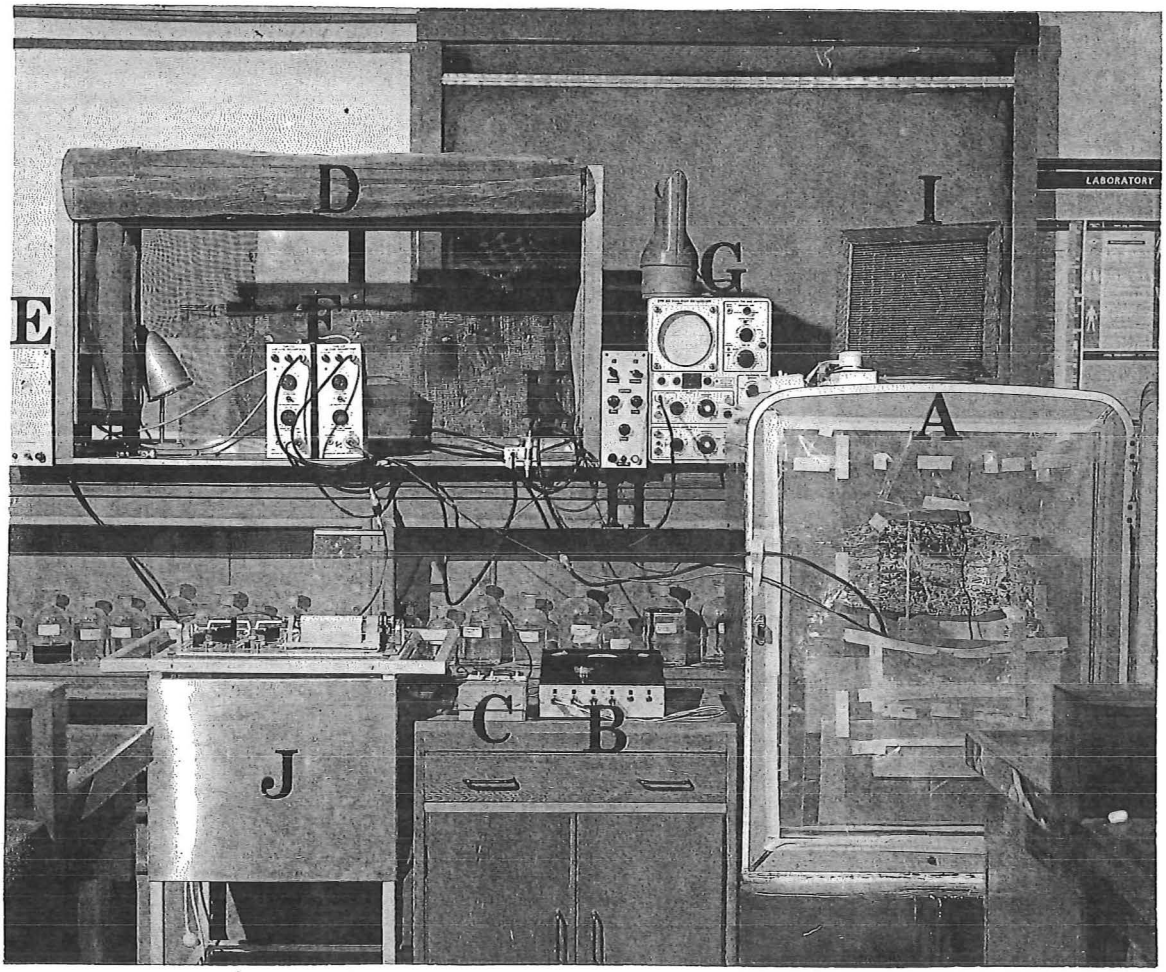
The experimental period began after the building of an outdoor terrarium. The 4' x 6' x 8" open terrarium was situated on the roof of the Zoology Building where the skinks were exposed to the prevailing weather and photoperiod. The same food was available ad libitum in addition to a large variety of arthropods which were attracted to the terrarium. These included Hymenoptera, Diptera, Coleoptera, Lepidoptera, and arachnids. The extent to which these exogenous sources of food were utilized is not known. Soon after the grass grub beetle (Costelytra zelandica) was seen in the terrarium, however, their elytra were found in skink faeces (deposited during fasting in the laboratory). The food station was sheltered from direct insolation and rain (Figure 2). Since cover was provided, the skinks were usually concealed just as in the field.

## B. EXPERIMENTATION

The research period consisted of two distinct phases. During the preliminary phase (April to October, 1970), skinks were captured and observed, equipment was designed, constructed and tested, and procedures were tested. When time, space and equipment became available, the experimental phase was initiated. All the data included in this report are from the period November 1970 to January 1971.

### 1. Thermometry

During the experimental phase, the skinks were housed in the outdoor terrarium. In an effort to determine a large number of body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J
LABORATORY

FIGURE 3

Equipment for EOG and Heating and Cooling Experimentation.

A. Temperature Cabinet

B. Thermistor Unit

C. Preparation (skink), see Figure 5 for a close-up.

D. Faraday Cage

E. Power Supply for Preamplifiers

F. Preamplifiers

G. Oscilloscope

H. Audio amplifier

I. Speaker

J. Hewlett-Packard Preamplifier and Recording System

K. Switches

Note: The details of the electronic apparatus are given in Figure 4.

temperatures ($T_B$*) during a variety of weather conditions and times of day that would be meaningful and could be related to the skinks' thermal relations in the field, similar components to those of the spit habitat were placed into the terrarium. The object was to create a simplified environment with a restricted number of microhabitats but a wide range of microclimates. Included in the terrarium were a tussock of pingao, spit sand, a feeding station, pieces of foam rubber (the latter chosen in preference to driftwood for its thermal properties, low specific heat and low thermal conductivity), some rocks, and a water tray.

Some field temperatures were taken, but the success of this method for determining the thermal relations of lizards is limited by their habits and their population densities. Another difficulty in the field is that of measuring the ambient temperature ($T_A$) of a microhabitat which is occupied by a skink. Because of the exceedingly large number of microhabitats, the probability of finding an occupied one is extremely low; once a concealed lizard has been located and captured, the microhabitat has been disturbed and cannot be accurately measured. The $T_B$ of a lizard is not necessarily the same as the $T_A$ of its microhabitat.

After a few weeks of adjustment of the lizards to their new milieu, the experiment began. The procedure used was as follows: first, the $T_A$ of microhabitats where skinks might be concealed were measured and, secondly, the objects were lifted and the $T_B$ of any skinks found underneath were measured intracloacally.

All the temperatures taken in the terrarium, laboratory and the field were measured with the same Thermistor Unit and thermistors (Figure 4 includes a block diagram of the circuit of the Unit). It was a modified Wheatstone bridge, designed and constructed by Depart-

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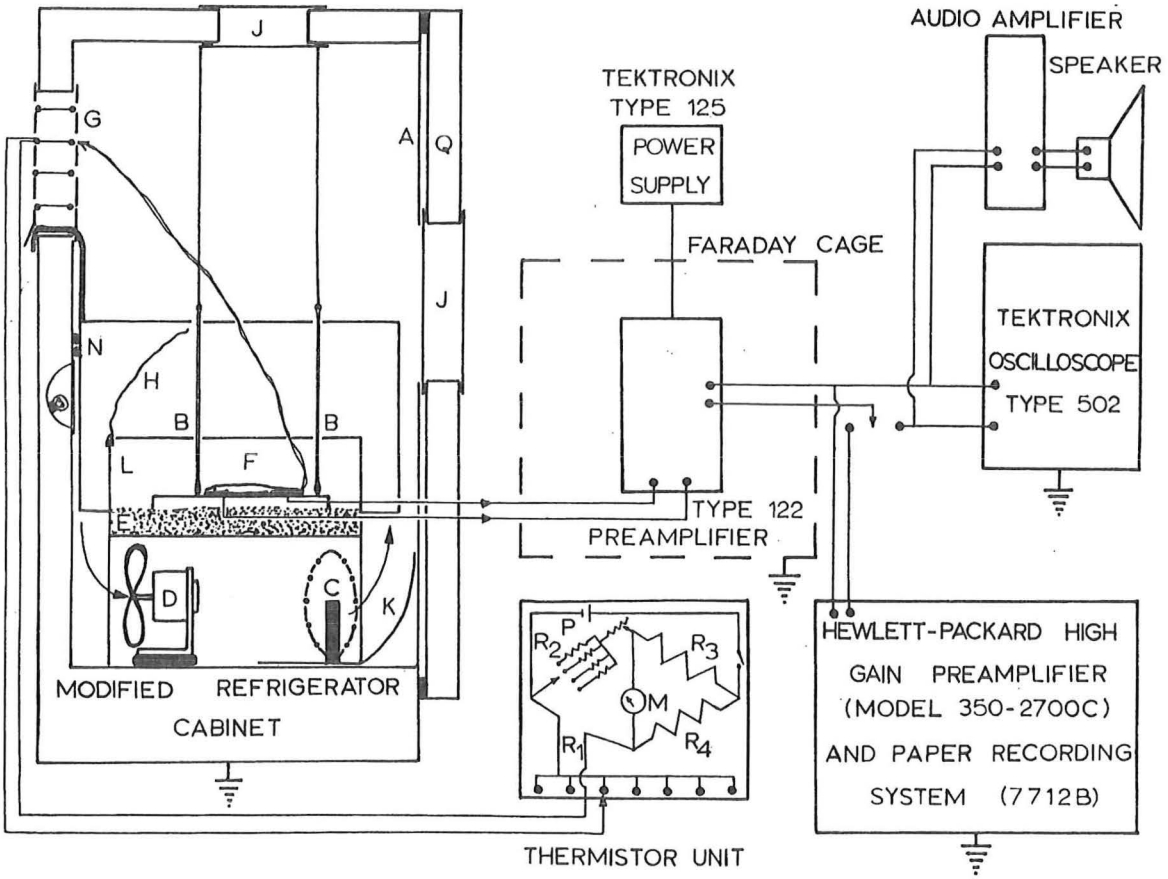
* All capitalized abbreviations are used for the singular and plural of the nouns abbreviated.




SCHEMATIC DIAGRAM OF EOG APPARATUS

FIGURE 4

SCHEMATIC DIAGRAM OF EOG APPARATUS

A. Polyethylene cover

B. B. Mercury-in-glass thermometers

C. 500 watt heater

D. Fan (mounted on hard rubber)

E. Kaitorete Spit sand

F. Preparation (skink) taped onto balsa wood stretcher lying on a dissection board

G. Panel containing plugs for thermistor leads (jacks)

H. Aluminium foil shield for cooling coils on back wall. On both side walls, aluminium panels cover cooling coils.

J. J. Double 'Perspex' observation windows

K. Aluminium heat and air deflector

L. Aluminium box (terrarium) and stand

M. Microammeter

N. Back wall with sealed lamp and cooling coils (in section)

P. Power source (Mallory cell)

Q. Door of temperature cabinet

$R_1$. Thermal resistor

$R_2$. Selection of four resistors and helipot

$R_3$ and $R_4$. Resistors of equal resistance

Note: Flow of air shown (by arrows) under terrarium and across heater coils.

mental Technicians. It consisted of a helipot, microammeter, and several fixed resistors selected to provide four overlapping ranges of thermoresistance response. All the thermistors (IK2 type) and mercury-in-glass thermometers used in this study were calibrated in a Grant thermostatic waterbath (accurate to ± 0.01 °C) against a Braun 'Warburg' thermometer (accurate to ± 0.05 °C). The small head thermistors used are characterized by their high rate of resistance change, a large negative temperature coefficient of resistance and by low conductivity. The calibration curves of the thermistors were checked on three occasions during the study. No change occurred, attesting to their accuracy and stability against aging. Because of their rapid heating and cooling, small terrestrial vertebrate ectotherms (T.V.E.) must be measured rapidly and with a minimum of contact. To minimize heat conduction from the hand during $T_B$ recording, a rubber glove was worn, and the $T_B$ was taken within ten seconds. The skink was held just behind the head and by the tail. A check against heat gain to the skink was possible due to the sensitivity of the Thermistor Unit; the microammeter needle could not be balanced during heat exchange. From preliminary experiments, it was determined that when the thermistor probe was inserted into the cloaca about 4 centimetres (depending on the size of the subject), it moved up the large intestine and lay well within the abdominal viscera. This temperature was assumed to be the average $T_B$.

2. Heating and Cooling

Terrestrial vertebrate ectotherms, which include most reptiles and some amphibians, (T.V.E.) are characterized by having a variable $T_B$ (poikilothermic); saurians are also largely thermophilic whereas amphibians are cryophilic. Given a rapidly fluctuating thermoenvironment, the body of a thermophilic T.V.E. will be undergoing rapid heat exchange with its milieu. The physical and biological effects of heating and cooling are important to an understanding of the thermal relations of an organism.

a. Calorimetry (Thermal Properties)

The thermal relations of organisms are closely related to their

water balance. This is because the thermal properties of organisms are largely determined by the thermal properties of water.

i. Specific Heat (S.H.)

The specific heat (k) of a body is defined as the ratio of changes of heat content (dQ) to the product of the mass (m) and the temperature difference (dT).

$$k = \frac{dQ}{mdT}$$

A simple calorimetric method was used, employing a water calorimeter consisting of a thin-walled copper can with a cover through which a thermistor and a copper wire stirrer were passed. Heat loss was reduced by surrounding the can in a jacket of expanded polystyrene leaving a dead air space in between. The weights of the can and stirrer ($m_c$), water ($m_w$), and the dead skink ($m_s$) were obtained to a tenth of a gram on a Mettler balance. The water temperature was recorded before ($T_1$) and after ($T_2$) the warm skink was placed into the calorimeter. Knowing the S.H. of water ($k_w$ = 1.00 calories/gram $^{o}$c) and of copper ($k_c$ = 0.093 cal./gm $^{o}$C), the S.H. of a skink ($k_s$) can be determined by the following relation:

$$m_s k_s (T_s - T_2) = m_w k_w (T_2 - T_1) + m_c k_c (T_2 - T_1)$$

heat liberated by skink | heat absorbed by water | heat absorbed by the calorimeter

therefore: $$k_s = \frac{m_w + 0.093\, m_c (T_2 - T_1)}{m_s (T_s - T_2)}$$

At the beginning of the experiment, the water temperature was at room temperature to reduce heat exchanges between the calorimeter and the laboratory air. The freshly killed skink with a thermistor in its cloaca was placed into a boiling tube and heated in a hot waterbath at 50 $^{o}$C. When its $T_B$ was 50.0 $^{o}$C, it was placed into the calorimeter. Autolysis was minimized by rapid heating and cooling. Temperature readings were taken every 15 seconds to obtain the highest rise in the temperature of the system ($T_2$). Thermo-

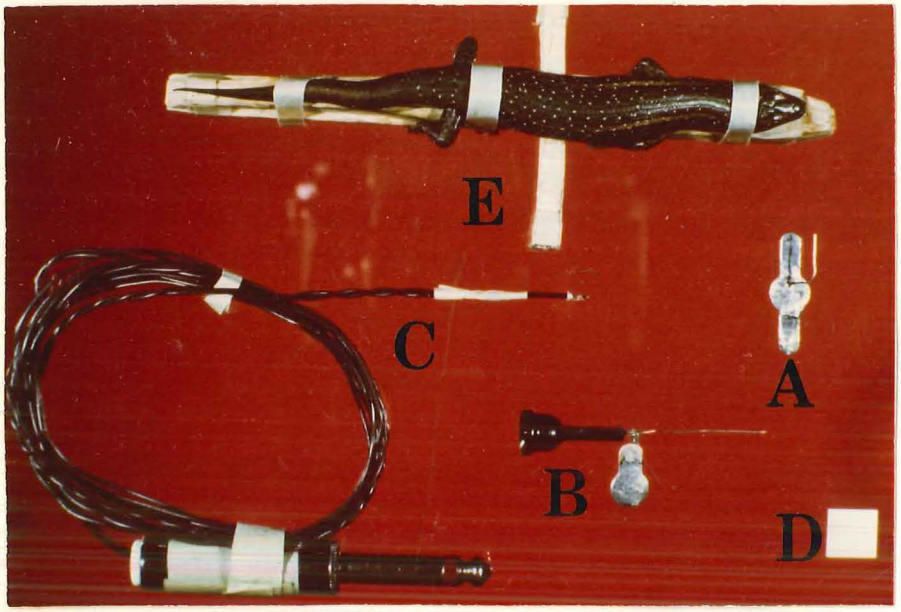
equilibrium took only five to ten minutes because of the high heat capacity of water, so that it was not necessary to correct for changes in atmospheric pressure changes nor for heat loss using a cooling constant for the calorimeter. The rate of cooling of the calorimeter commencing with a temperature differential of 2 $^{o}C$ (about four times the differential caused by introducing the warm skink) was not measureable over a ten minute period with the temperature recording apparatus used.

ii. Thermal Conductance

A body, living or inert, may exchange heat with its environment by three distinct processes: conduction, radiation and convection. Because of the thermal properties of still air (low thermal conductivity and low specific heat), the heat lost by a body is largely by radiation and by free convection (bouyancy effect). These heat exchanges are governed by Newton's Law of Cooling which states that the loss of heat is proportional to the amount by which the $T_B$ exceeds the $T_A$ (temperature excess). This law is known to be approximate and of limited application but it is a satisfactory statement of affairs for physiological studies. At a $T_B$ above 0 $^{o}K$, all bodies emit electromagnetic radiation. The nature and intensity of the radiation from a body depends on its $T_B$ and on the nature of its surface. In general, as $T_B$ increases, the total energy radiated increases, the wavelength of maximum intensity moving toward the shorter wavelengths. At room temperature, radiation is very largely in the range of the infrared (1 - 15 $\mu$). The rate of heat transfer ($dH/dt$) is determined by the temperature difference between the animal ($T_B$) and its environment ($T_A$) and by a constant (C) for a particular body.

$$\frac{dH}{dt} = C\ (T_B - T_A)$$

When the specific heat (k) is known, the rate of change of $T_B$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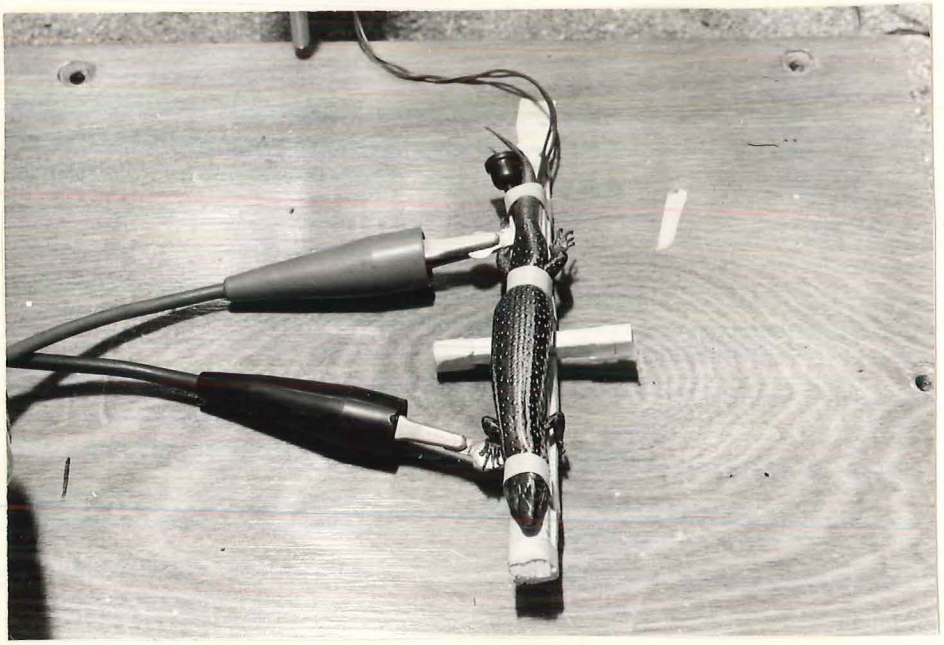

FIGURE 5

Skink on stretcher with electrodes and thermistor displayed.

A. Active electrode
B. Indifferent (ground) electrode
C. Bead thermistor and jack
D. One centimetre square
E. Subject on balsa wood stretcher

FIGURE 6

Skink on stretcher in the temperature cabinet with electrodes and alligator clips in place.

$(dt_B/dt)$ can be determined from the temperature difference and the constant C/k:

$$\frac{dt_B}{dt} = \frac{C}{k}(T_B - T_A)$$

By integration, $\log (T_B - T_A) = \frac{C\ t \log e}{k}$, where e = base of natural logarithms. When $\log (T_B - T_A)$ is plotted against the time, the value C is determined by the slope of the resulting curve multiplied by k/log e (Morrison and Tietz, 1957). The value C (thermal conductance), measured in calories/gram/hour/$^{o}$C, is dictated by the body shape, size and surface characteristics.

A seven cubic foot commercial refrigerator was renovated to provide a relatively constant $T_A$ over a wide range of temperatures from below 0 $^{o}$C to over 40 $^{o}$C. The temperature cabinet was fitted with a fan, heater, terrarium, cooling coils on the side walls, thermostatic control, and observation windows (Figures 3, 4). The large heat transfer which would have occurred when the door was opened was reduced substantially by taping a heavy piece of polyethylene over the opening with a small hole through which the subject was passed. $T_A$ were monitored using strategically placed Hg thermometers and thermistors, so that temperature oscillations could be dampened. The heater and fan or the cooling unit could be activated independently and quickly in response to an expected or actual deviation from the set point. Once the $T_A$ was stabilized, however, it could be maintained to within $\pm$ 1 $^{o}$C. The temperature range selected for the heating and cooling experiments was 5 - 35 $^{o}$C. Preliminary data suggested that this range would be about the maximum temperature differential that the skinks would experience in the field, eg. during the winter. Because of their habits, they could probably avoid a $T_B$ below 5 $^{o}$C by burrowing and above 35 $^{o}$C by being in the shade.

For heating and cooling experiments, the subject was taped onto a stretcher (Figure 5, 6). The cross-shaped stretcher, which was constructed of balsa wood pieces, was designed to be a stable jig into which the active electrode could be inserted and onto which

the skink, thermistor and indifferent electrode could be taped. For the cooling experiments, the subjects were equilibrated in a waterbath set at 35 °C. The waterbath apparatus consisted of a 46 litre waterbath with heavy plastic secured tightly over the water surface. A circle was cut out of the plastic and an aluminium cake tin was sealed into it so that the tin was completely surrounded by water but the inside of the tin was moisture free. A weighted foil-lined piece of plywood was placed over the waterbath so that it could be slid back far enough to insert a subject on its stretcher. The water was heated and circulated by a Tempunit (TU 8 from Techne Ltd.). These units are a combination heater, thermostat, stirrer and centrifugal pump and they are able to maintain the $T_A$ to within 0.1 °C of the set point. Once the $T_B$ had become stabilized, the subject was quickly placed into the temperature cabinet which was at 5 °C. The $T_B$, and occasionally ECG and ventilation counts, were taken every minute and the $T_A$ monitored until the $T_B$ was within a degree of the $T_A$. The time course of the experiments was measured by a stopclock (Griffin and George, Ltd.). The accuracy of this time piece was checked against a 30-second stopwatch which was presumed to be the more accurate of the two time pieces; they did not differ significantly.

In an effort to run a heating trial immediately after a cooling trial and after stabilization of the $T_B$ at 5 °C, most skinks were placed in the waterbath for re-heating. The procedure of using the waterbath for the heating trials was abandoned when it was decided that some of the differences between the rates of heating and cooling could be due to the different components of heat exchange. Since other investigators have had two temperature cabinets, the possibility of different kind of heat exchange had not arisen. In subsequent trials, the skinks were stabilized at 35 °C in the waterbath, cooled to 5 °C (cooling trial), held in the laboratory refrigerator at 5 °C until the temperature cabinet was heated to 35 °C, then it was transferred to the cabinet for re-heating (heating trial). For heating and cooling of dead skinks, they were weighed and taped

onto a stretcher, equilibrated at 35 °C as usual, then killed with chloroform and quickly placed into the cabinet at 5 °C (cooling trial) and cooled to 5 °C. The dead skink was re-heated as above. This method reduced the possibility of autolysis. Live and dead subjects were chosen to include the full range of weights of captured skinks.

b. Electroorganography (EOG) *

EOG is the recording and measuring of electrophysiological (EP) phenomena in organs, or in organised tissues associated with a biological function. During the past several decades, EP techniques have been applied to many biological phenomena including: vision (electroretinography), smell (electroolfactography), cortical activity (electrocorticography), as well as the more familiar applications ECG, EEG, EMG, and others. When the EOG is recorded at the surface of the body, it is necessary to distinguish between the potential changes which occur in any muscle prior to contraction or nerve during conduction and potentials arising in the heart or other organs. In this study, EP techniques were used to measure the electrical responses of the heart (ECG) and of the intercostal muscles associated with ventilation (electropneumography or EPG +) under stressful (heating and cooling) and standard (equilibration) conditions. Because these techniques were applied to a greater extent in equilibration experiments, only relevant procedure will be presented in this section. The apparatus is illustrated in Figures 3 - 6.

When ECG were taken, the recording began immediately after the subject had been transferred to the cabinet for heating or cooling

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* This generic term was coined because of the lack of another term.

+ EPG, unlike the usual EMG, occurs as discrete bursts of ~~action potentials~~ electrical activity occurring which can be linked to a specific physiological function rather than as biological noise. This term was also coined.

and was continuous except for the thermistor readings taken each minute. Because of the difficulty of monitoring all the apparatus single-handed, either ventilation or heart response was measured at any one time. The high frequency action potentials of the thoracic musculature associated with ventilation were converted into sound using an audio amplifier and the ventilation rate was determined using a desk counter and a stopwatch. The heart rates were calculated from the ECG after the experiment.

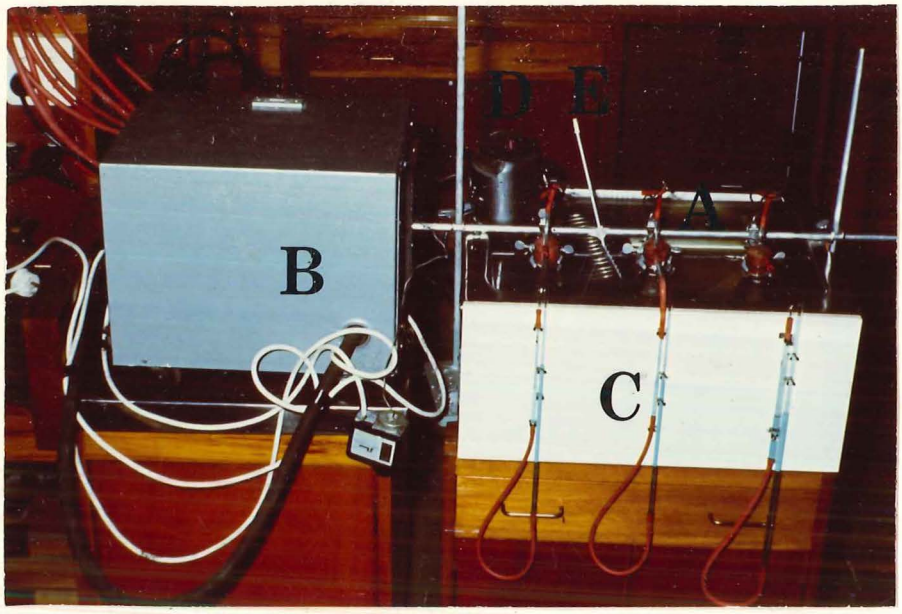
3. Equilibration Experiments

In an equilibration experiment, the subject is allowed to come to thermoequilibrium with a selected experimental $T_A$. After this condition has been reached, recording commences. In such an experiment, standard conditions are usually also observed, i.e. the subject is fasted and under conditions of minimal activity and stress. Even though ectotherms become biological artifacts under these conditions, it is an essential physiological technique (Bartholomew, 1969).

a. Respirometry

All physiological processes are energized by metabolic reactions which ultimately require oxygen. A convenient measure of the metabolic rate (M.R.) of an organism is therefore oxygen ($O_2$) consumption. Although standard (S.M.R.) and basal (B.M.R.) metabolic rates are obtained using fasted, quiescent subjects, the latter terminology is applied to endotherms since $T_B$ remains constant as the $T_A$ is varied. S.M.R., on the other hand, are determined for ectotherms where $T_B$ changes with the $T_A$.

A simple, constant pressure-closed-manometric system was used to determine the $O_2$ consumption of L. lineoocellatum. Three 46 litre waterbaths each with a Tempunit and three manometric units including one control (thermobarometer) and two experimental units were employed (Figure 7). Each unit consisted of a graduated arm (stationary), a movable arm, and a 250 ml. flask (containing sand and about four grams of Carbasorb soda lime wrapped in cheese cloth and suspended above the sand) and was arranged as shown in Figure 8.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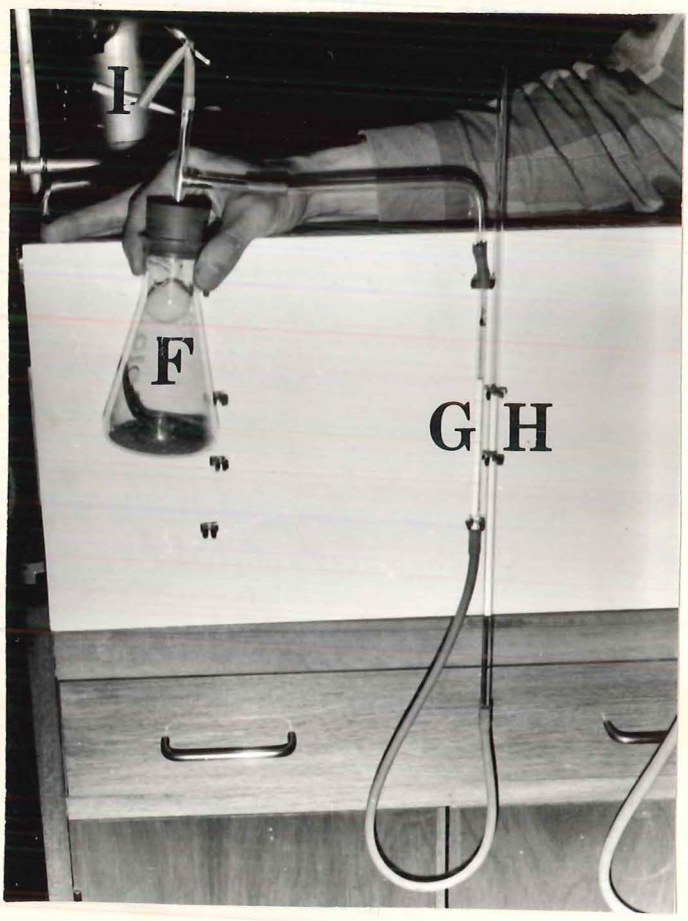

I
F
G
H

FIGURE 7

Respirometry Apparatus.

A. Water bath

B. Refrigerator Unit and coil

C. Three manometer units, the right one was the thermobarometer.

D. Tempunit, combination stirrer, heater and thermostat.

E. Mercury thermometer

FIGURE 8

One manometric unit.

F. Flask containing sand, $CO_2$ absorbant, and skink.

G. Stationary, graduated manometer arm.

H. Movable manometer arm.

I. Rubber flush tube doubled over and held by a Mohr clip.

The graduated arms were 2 ml. pipettes which could be read accurately to 0.01 ml. The fluid in the manometers was coloured water with detergent to reduce the surface tension.

All subjects were fasted for three days prior to being used in an experiment. After an hour of thermoequilibration of the water, flasks and weighed subjects, the rubber flush tubes were doubled over and clamped with Mohr clips. The heights of the fluid in the arms were levelled and recorded and the stopclock was started. As the skinks consumed $O_2$ and the expired $CO_2$ was absorbed by the Carbasorb, the volume in the graduated arm decreased by a volume equivalent to the $O_2$ consumed. The pressure inside the flasks was readjusted to the air pressure within the laboratory by raising the movable arm. The volume recorded was corrected for barometric changes by adding the change in volume of the thermobarometer over the same period when the latter had decreased and subtracting it when the volume had increased. The duration of the trial and the volume change were recorded when the manometer fluid approached the 2 ml. mark. By recording the barometric pressure in the laboratory using a Fortin barometer (which could be read to 0.01 mm. of Hg) before and after each trial, the average barometric pressure could be used to compute the S.M.R. at STP (760 mm. of Hg and 0 $^{o}$C). The main source of error is the lack of a completely closed system. This possibility was avoided by constant surveillance and adjustment of the fluid heights. In addition, a very thin film of petroleum jelly was applied to the rubber stoppers of the flasks to produce an airtight seal. The efficiency of the latter procedure was checked at the beginning of each series of determinations by raising the movable arm and increasing the internal pressure in the flasks. Ten minutes was sufficient time to detect changes in fluid levels due to leaks.

Determinations were made at 5-7, 13, 20, 27, 30 and 35 $^{o}$C. for the $T_A$ at room temperature or higher, only the Tempunits were required to regulate the $T_A$. For the lower $T_A$, a refrigerator unit and coil were used in addition to the Tempunits (Figure 7). Since

only one coil was available, it was shuttled between the three waterbaths. Since the temperature differential between the 13 °C waterbath and the laboratory $T_A$ was not great, this temperature never deviated more than 0.3 °C above the set point. It was difficult, however, to maintain three waterbaths exactly at 5 °C. It took about a day for the waterbaths to be cooled to 7 °C and a further day to obtain 5 °C. An elaborate system of centrifugal pumps (of the Tempunits) and siphon tubes linking each bath with the other two was used to maintain the water levels and to circulate the water in the baths. The flow of water from the pumps was adjusted by screw clamps to a rate of 1.2 litres/minute. The $T_A$, once stabilized, was maintained within a degree.

Skinks were selected to include a wide range of weights. During periods when no determinations were made, the subjects were kept in the laboratory at room temperature (17 - 23 °C) with only water available. When subjects were not used during periods as long as a few weeks, Tenebrio larvae were available ad libitum until three days before the skinks were used in experiments.

b. EOG Experimentation

As with the preceding experiment, standard conditions were used, and all rate-temperature (R-T)† data were acutely* measured. No anaesthetic was used since it would have introduced another variable and an unnecessary artifact. Each subject was weighed before a trial, taped onto a stretcher and cooled rapidly to 5 °C (cooling trial), then the subject and the cabinet were equilibrated at 0 °C for at least an hour before recording. The subject was equilibrated to subsequent $T_B$ at five degree intervals to 35 °C providing that 'noise' was not obliterating the EOG tracings. The $T_A$ of the cabinet was monitored using calibrated Hg thermometers and thermistors (Figure 4). The hour of thermo-equilibration before recording was largely for the benefit of the large mass of the inside of the cabinet but, once a $T_A$ was stabilized, it could be regulated within a few tenths of a degree.

† Read as, rate with respect to temperature.

* That is, measured over a short time, unlike chronically measured date such as from acclimation experiments (Bullock, 1955).

During preliminary experiments, several leads and lead positions were tried. The subcutaneous and especially the intramuscular limb leads were found to cause discomfort and stress as indicated by the frequency of struggling and the amount of EMG recorded. The large size and weight of the alligator clips pulling on the limbs directly was avoided by soldering platinum wire (28 s.w.g.) onto metal tags which fitted between pieces of balsa wood that formed the stretcher (Figures 5, 6). The active electrode was inserted subcutaneously antero-ventral to one of the forelimbs. At autopsy, the electrode was found to lie ventral to the auricles or the AV junction depending on the orientation of the platinum wire. The indifferent (ground) electrode was inserted with the thermistor into the cloaca. These leads, although somewhat unconventional, were the least stressful and the easiest to use, and produced consistent analyzable tracings.

The bioelectric signals from the skink were amplified by approximately 1000 X, before being fed into either the oscilloscope and audio amplifier, or the Hewlett-Packard (H-P) System depending on whether the EOG was being monitored or recorded (Figures 3, 4). The frequency response of the Tektronix Preamplifier was set to permit the maximum frequency range with the minimum of noise and drift. This was 0.8 or 8 cycles/second (low frequency cutoff) and 50 or 250 c.p.s. (upper cutoff). The input signals could have been single-ended or push-pull for feeding into the Tektronix Preamplifier. Push-pull input was found empirically to produce the best results and the minimum noise from mains interference. Coaxial cable, used between apparatus, also reduced interference. The audio amplifier picked up high frequency signals coincident with the thoracic movements (ventilation) and occasionally 'RS' sounds from the heart (ventricular systole).

The H-P Preamplifier was equipped with AC and DC input jacks. The signals from the Tektronix Preamplifier could be fed into either of these jacks where it was amplified at a gain of 20,000 and 20 respectively. The resultant signal was then attenuated at maximum sensitivity until a suitable deflection of the stylus of the

recorder was obtained (Figure 9 F). In this study, the DC input jack was used. Attenuation reduced the input signals by discrete ratios, eg. X1 (no change), X2 (signal cut in half), X5, X10, X20 and others. The frequency response of the H-P Preamplifier was set at 0.04 KC and, because it had no low frequency cutoff, the response extended theoretically down to zero c.p.s. The upper cutoff filtered most of the 50 c.p.s. mains interference, but not its own (Figure 9 A). The low frequency cutoff of the Tektronix Preamplifier filtered low frequency signals before they were fed into the H-P System.

An internal one-second timer was used for integral timing. There was no difference between the timer and a 30-second stopwatch for accuracy, but both were more accurate than the ruled temperature sensitive Permapaper for determining the durations of cardiac events. A calibration switch inserted a 50 mV signal into the H-P Preamplifier which had the same effect as a 50 mV signal into the DC input jack. This signal produced a deflection of 19.5 mm. at maximum sensitivity, i.e. one centimetre deflection equalled 25.6 mV. Because the bioelectric potentials were preamplified approximately 1000X, one centimetre deflection was equal to the following bioelectric voltages.

TABLE I : Bioelectric potentials as a function of attenuation and deflection.

| Attenuation | Final Amplification | Bioelectric voltages (μV |
|---|---|---|
| X 1 | 1000 X | 1 centimetre ≈ 26 |
| X 2 | 500 X | 51 |
| X 5 | 200 X | 130 |
| X10 | 100 X | 260 |
| X20 | 50 X | 510 |

Recognizable waveforms were obtained using the leads and apparatus described above. The measurement and interpretation of these intervals and waves were based on Burch and Winsor (1960), Dawe and Morrison (1955), and Schaefer and Haar (1962) and are summarized in Table III. From the better recordings, P-R, R-T, and T-P intervals and RS, P, and T waves were measured using calipers accurate to $\pm$ 0.1 mm. The accuracy of the duration of these events depended on the paper speed used.

TABLE II : Duration accuracy in relation to paper speeds.

| Paper speed | Accuracy |
|---|---|
| 2.5 mm./sec. | 0.1 sec. |
| 5.0 | 0.05 |
| 25.0 | 0.02 |
| 50.0 | 0.01 |

The durations of the electrocardiac events were measured using the beginnings and ends of the predominant waveforms. In the literature, however, peak-peak distances are usually measured but as a matter of convenience or of necessity (due to the quality of the ECG). This measurement can be grossly inaccurate even for ECG of the same animal at different $T_B$ (Figure 29). There is considerable variation in the slopes and forms of waves (Figure 31). Lack of information regarding the spatial-temporal relations of conduction through the reptilian heart makes the interpretations of the events conjectural but not untenable (Table III is based largely on the mammalian myocardium). By analogy with mammalian ECG, it appears certain that the beginning of the P wave signals the beginning of the depolarization of the auricles with the individual fibres

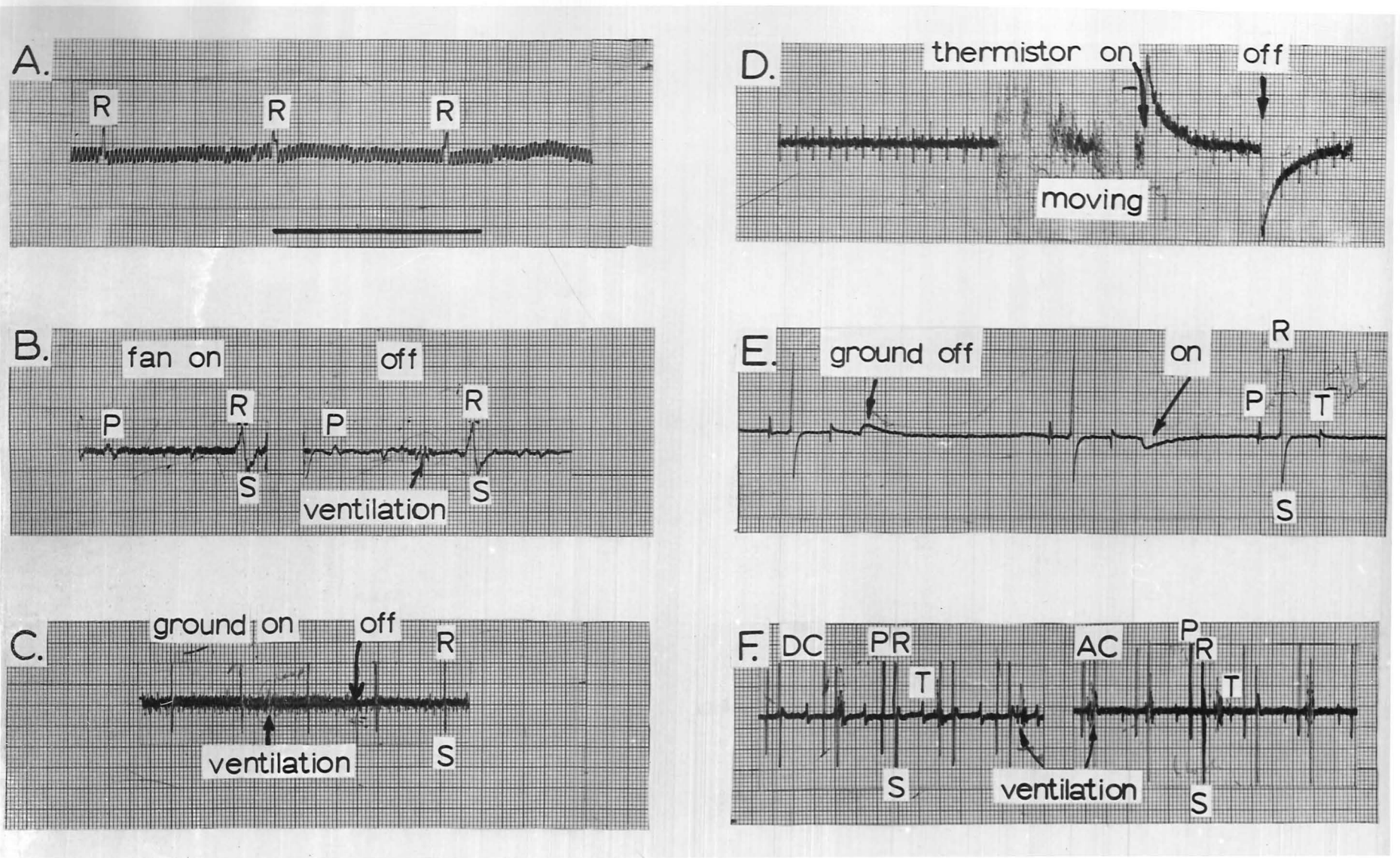

A.
R
R
R
B.
fan on
off
P
R
S
P
R
S
ventilation
C.
ground
on
off
R
S
ventilation
D.
thermistor on
off
moving
E.
ground off
on
R
P
T
S
F.
DC
PR
T
S
ventilation
AC
P
R
T
S

FIGURE 9

Electroorganograms showing noise and interference.

A. 50 cycle interference

B. Effect of turning fan (inside temperature cabinet) on and off.

C. Effect of removing all grounds to Faraday cage (at arrow).

D. Effect of Thermistor Unit being turned on and off with a deflection of approximately 400 μV and Common Mode returning trace to the baseline.

E. Effect of taking ground from temperature cabinet to oscilloscope off and the reverse procedure. Deflection is about 30 μV.

F. Effect of recording signals fed into the DC jack (X 2 attenuation) and signals from the same subject fed into the AC jack of the H-P Preamplifier (X200 attenuation).

contracting soon after their depolarization. Similarly, the beginning of the RS wave appears to coincide with the initiation of ventricular depolarization and the end of the T wave with the end of repolarization and of ventricular contraction. It is generally agreed that the T wave of the auricles ($T_a$) signalling the repolarization of the auricles occurs simultaneously with ventricular depolarization and its effect is therefore masked. The Q wave, occasionally found in reptilian and mammalian ECG was not found for L. lineoocellatum using the leads and positions described above. There is no satisfactory interpretation for the Q wave even for human ECG. Even on the clearest tracings of this skink, there was no evidence of the sinus venosus (SV) wave which Furman (1960) described for the clawed toad (Xenopus laevis). Mullen (1967) found this wave most frequently on snake ECG (about 25% of the records), whereas it was detected in less than 10% of lizard ECG studied.

A problem of special importance in EP is the pickup of unwanted signals or noise by the preparation and electrodes, in particular the 50 cycle mains voltage (Figure 9 A). Conductors carrying AC give rise to associated electric and magnetic fields having characteristic space-time distribution. In addition, impulses from switching other apparatus or putting grounds on and off generally have components in the frequency band used (Figures 9 B, D, E). The first problem is reduced by the choice of bandwidth, by the design of the equipment (push-pull, differentially balanced circuitry) and by the use of a Faraday cage, shielded cables and grounds. Grounds usually work most effectively when all apparatus is grounded to the same point. For effecting rapid ad hoc ground connections between apparatus and the Faraday cage, lengths of insulated flexible wire with crocodile clips at each end were used. The cage was grounded to the copper pipe of the cold water system. On the best recording days, changes in the grounds would not affect the trace other than to produce a single potential (Figure 9 E).

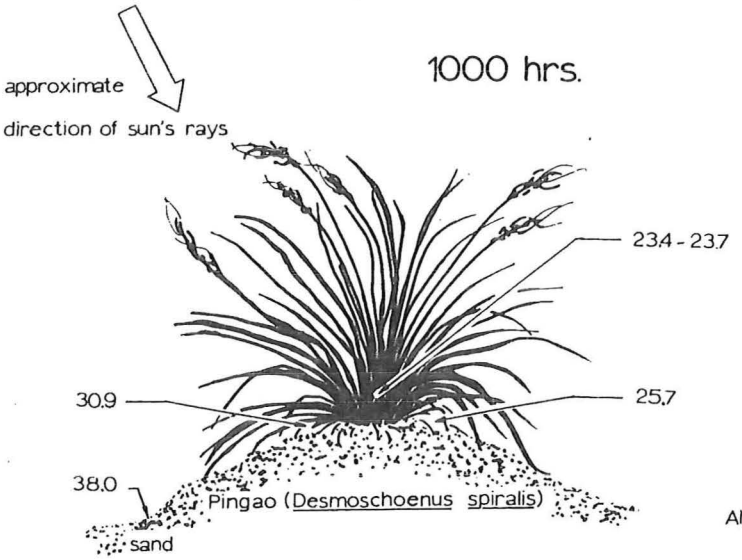
TABLE III : DESCRIPTIONS AND INTERPRETATIONS OF CARDIAC EVENTS*

| Cardiac Event+ | Description | Interpretation |
|---|---|---|
| P-R interval | Beginning of P wave to beginning of R wave | Approximately the period of electrical activity of auricles |
| R-T interval (Q-T) | Beginning of R wave to end of T wave | Duration of electrical activity of the ventricles |
| T-P interval average | Difference between the average R-R and P-T intervals | Quiescent period of myocardial activity and an inverse measure of SA node automaticity |
| P-R segment | End of P wave to beginning of R wave | Delay in transmission of impulse across AV junction or AV conduction time; when all auricular fibres are depolarized |
| S-T segment (RS-T) | End of S wave to beginning of T wave | Duration of excited state of ventricular muscle or when all ventricular fibres are depolarized |
| P wave | Beginning to end of P wave | Depolarization of auricles |
| RS wave (QRS complex) | Beginning of R wave to end of S wave | Depolarization of ventricles |
| T wave | Beginning to end of T wave | Repolarization of ventricles |

* Based on Burch and Winsor (1960), Dawe and Morrison (1955), and Schaefer and Haar (1962).

\+ Alternative designations for events are given in parentheses.

# KAITORETE SPIT NOV. 2, 1970




Leiolopisma lineoocellatum

32.2 29.4 30.5 30.8

L. zelandica

30.1 29.1 32.2 32.9

30.4 29.9

Hoplodactylus pacificus

28.2 27.5 26.9 26.1

32.0 (in sun)

All temperatures in degrees Centigrade

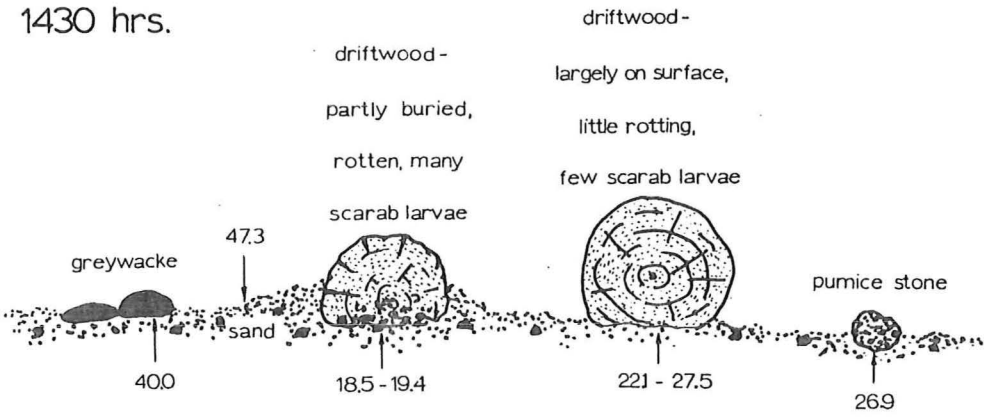


FIGURE 10

Microhabitats on a hot, sunny day in late spring on Kaitorete Spit. $T_B$ of skinks caught between 0930 and 1100 hours are given. Compare the $T_B$ of *L. lineoocellatum* on a similarly hot day October 30 (Figure 13, IV - 9) in the outdoor terrarium. Average $T_B$ were coincidently both 30.7 °C.

Changes in the grounds, during bad recording sessions, had little effect on reducing the noise on the EOG. There is no simple approach to obtaining records free from noise. Sometimes, for instance, there was more noise with grounds than without them (Figure 9 C). The second problem of electromagnetic interference is reduced by distance, i.e. removing the apparatus from the interfering fields, and by screening.

## RESULTS AND DISCUSSION

### A. THERMAL RELATIONS

#### 1. Study Area and Terrarium

During the day, the climate near the ground - which is composed of innumerable microclimates - is often difficult to characterize. This difficulty is a function of the variable heat sources and sinks, and the thermal properties of the materials which make up the microhabitats. The behaviour of the skinks and the nature of the substrate and vegetation determine the microhabitats available to L. lineoocellatum. The relevant habitats at the spit included the substrate-air interface, under and in pingao, and under objects (usually driftwood because of its low thermal conductivity). By measuring the $T_A$ of these microhabitats on a day of high thermal flux (insolation), an estimate of the range of $T_A$ in the spit habitat which are important to the thermoeconomy of these small ectotherms can be obtained. The thermal relations of the spit were characterized under near optimal conditions on a day in the late spring and are described in Figure 10. For the purposes of this discussion, 'optimal' weather conditions are clear sky, sunshine and little wind. It is quite possible that for part of such days during the year, the $T_A$ of the substrate surface at the spit are above the temperatures tolerated by the skinks. During the summer months, the substrate $T_A$ is above 35 $^{o}$C for as long as eight hours

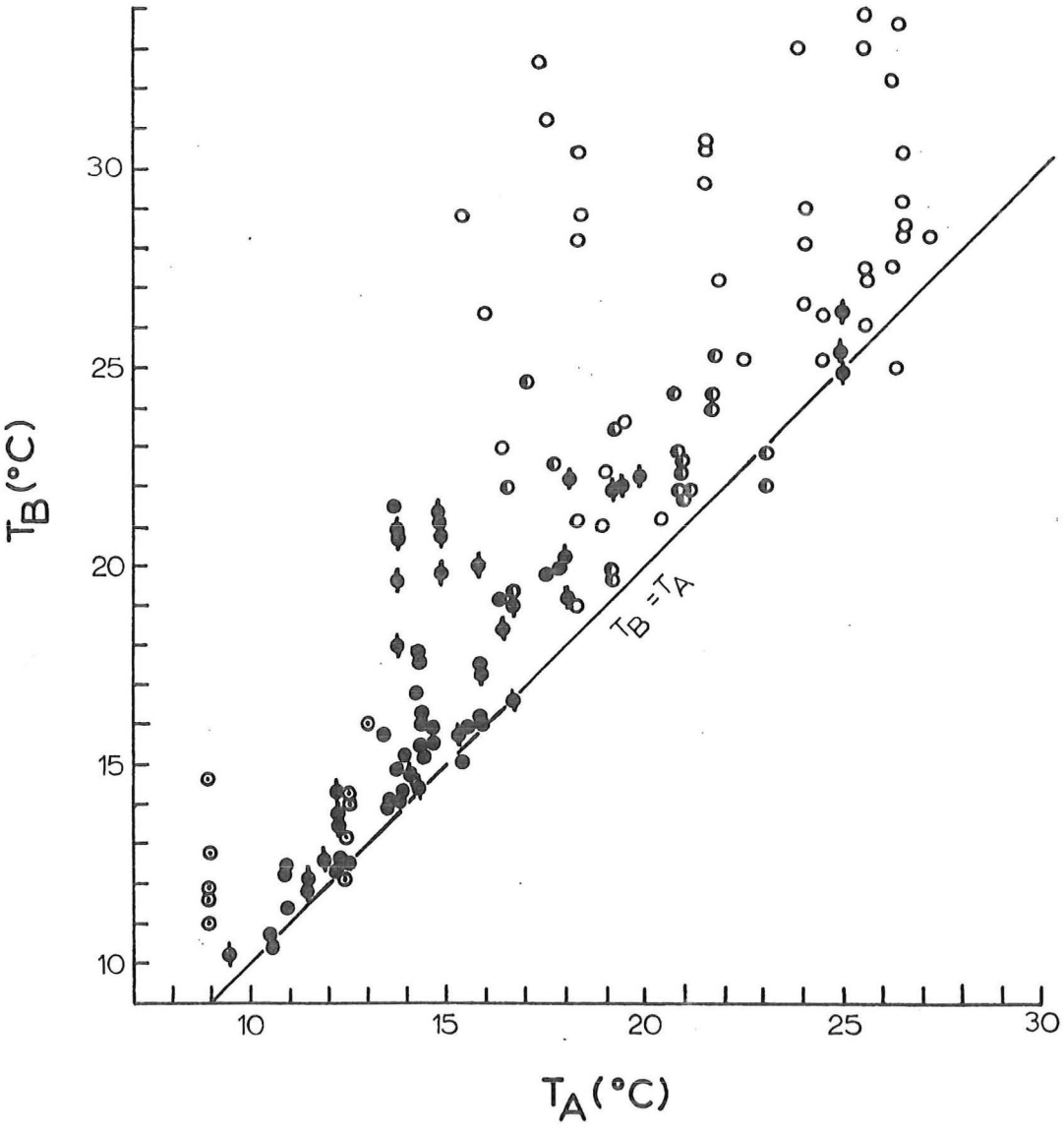

30
25
20
15
10
$T_B$ (°C)
10
15
20
25
30
$T_A$ (°C)
$T_B = T_A$

FIGURE 11

Relation of cloacal $T_B$ to the $T_A$ of microhabitats (in which skinks were found, but obtained before skinks were removed) in the outdoor terrarium during the period October 29 to December 1, 1970. The weather conditions are indicated by symbols: ○ - sunny, ● - mostly cloudy, ◐ - sunny with cloudy periods, ◍ - overcast and rainy, and ⊙ - clear late afternoon during sunny day.

under conditions of intense insolation. During these periods the skinks are concealed under objects and vegetation. Activity is limited to rapid locomotion - escape - to the nearest cover when disturbed. Normal activity would be restricted to early morning and late afternoon periods, i.e. they would tend to become crepuscular in habit during the summer. There is no evidence that L. lineoocellatum is strictly inactive during the night, but many scincids are considered diurnal particularly in their feeding and reproductive activity patterns.

The effect of shade in determining the $T_A$ around vegetation is evident from Figure 10, since there was about a five degree difference between the microhabitat under the tussock on the sunny side and the shady side. Because the stones at the spit were characteristically small and flat, they could not be used as cover on hot days. Lizards at the spit were not found under stones even during cooler parts of the day, suggesting that the stones were unsuitable cover for more than calorific reasons. The eroded sandstone rocks and boulders just above the high tide mark at Motunau Island, however, provided cover for a large population of lizards indicating that the size and thermal properties of the rocks are important criteria for their use as cover. The different thermal properties of greywacke and pumice are evident since the latter was fourteen degrees cooler underneath. The $T_A$ under driftwood depended on the size and the extent of submergence of the driftwood into the sand. An accurate $T_A$ under driftwood could be obtained by measuring the $T_B$ of scarab larvae. Because of their high water content and size, their $T_B$ was equal to the $T_A$ before the microclimate was disturbed. A temperature differential of almost 30 $^{o}C$ was obtained between the substrate and several centimetres below the surface under a piece of rotting driftwood. The skinks potentially had access then, to this differential within which to adjust their $T_B$ to conform to their preferred $T_B$ range.

When the terrarium was constructed, materials were chosen partly to mimic the spit habitat and partly to provide a similarly

wide range of $T_A$ under optimal conditions. By providing a relatively large number of microhabitats, it was hoped that none of the skinks in the terrarium would be forced to occupy unfavourable microclimates. A compromise had to be made, however, between the number of microhabitats provided and the number which could be measured in the hope of recovering each of the skinks in the terrarium over a short interval of time. By measuring these microhabitats before disturbing them, a meaningful $T_A$ was obtained. The cover was then lifted and the occupant (if any) was removed and its $T_B$ determined. In this way it was possible to determine the thermal relations of L. lineoocellatum. Table IV illustrates the range of $T_A$ of occupied microhabitats. The entry from 1200 hours on October 30 closely resembles the $T_A$ range obtained a few days later at the spit, attesting to the success of the construction of the terrarium's thermoenvironment (Figure 10).

2. Study Animal

The thermal relations of L. lineoocellatum were determined largely in the outdoor terrarium. Except for several $T_B$ obtained at Kaitorete Spit (Figure 10) and on Motunau Island (Figure 13), all $T_B$ were obtained under circumstances that permitted a measure of the $T_A$ of the occupied microhabitat prior to capture. The results of these data are summarized in Figures 11 and 12. Since measurements were made under suboptimal as well as optimal weather conditions, the macroclimatological data are included to illustrate the obvious effect of insolation on the thermal relations of these ectotherms. In most cases, when the skinks occupied microhabitats with $T_A$ greater than 17 $^{o}$C. insolation was an important factor in determining the maximum $T_A$ available and the range of $T_B$. Since $T_B$ were up to fifteen degrees above the $T_A$ of occupied microhabitats, the skinks had absorbed heat either heliothermically (basking) or thigmothermically (from the substrate), or most probably by both methods. Since all the skinks (except one) were concealed at the time of recovery, the temperature difference between $T_B$ and $T_A$

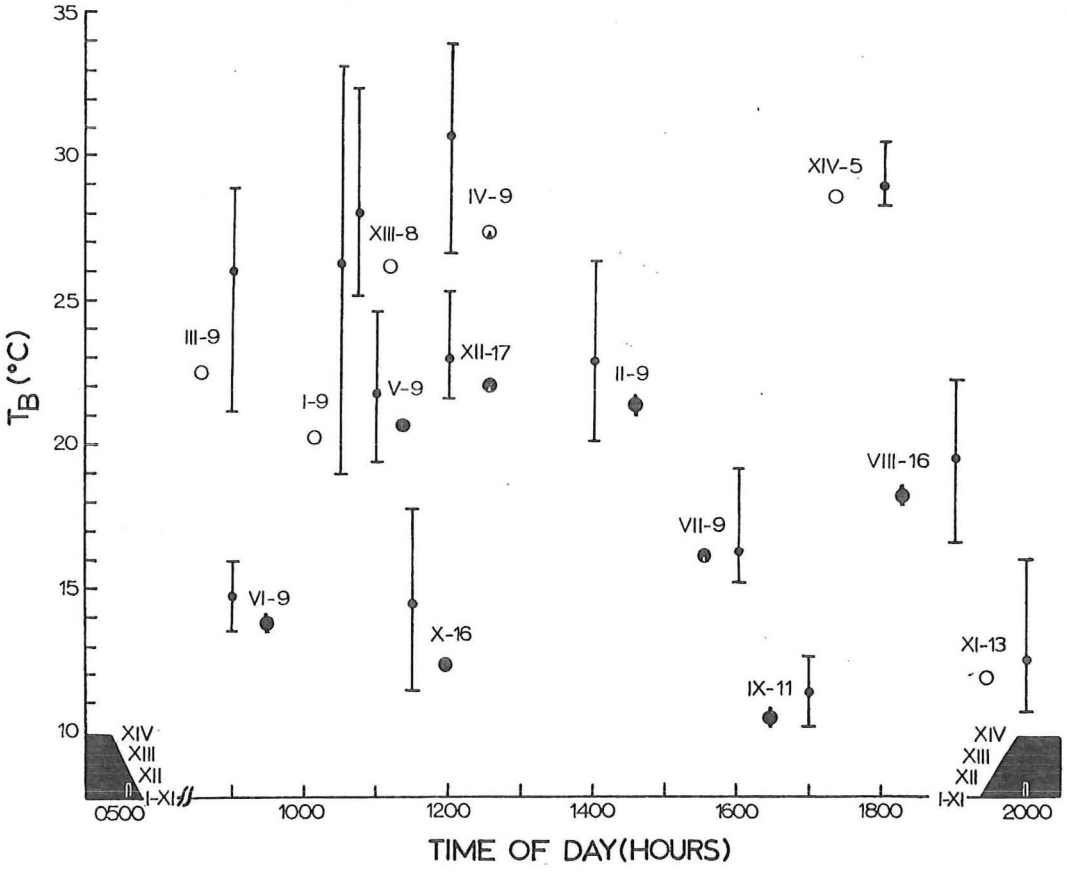

35
30
25
20
15
10
$T_B$ (°C)
III-9
I-9
XIII-8
IV-9
XII-17
V-9
VI-9
X-16
II-9
VII-9
IX-11
XIV-5
VIII-16
XI-13
XIV
XIII
XII
I-XI
0500
1000
1200
1400
1600
1800
2000
TIME OF DAY(HOURS)

FIGURE 12

Relation of $T_B$ to different times of day under various weather conditions. The mean $T_B$ and the ranges (vertical lines) are given. Roman numerals refer to specific recording situations characterized in Table IV and are followed by the number of skinks measured. Symbols: ○ indicates clear sunny weather with solid segments indicating approximate amounts of cloud cover in tenths to overcast conditions ● and rain ⬮. Sunrise and sunset times are indicated for the experimental period above the abscissa.

TABLE IV : Key to Figure 12.

| | Date | Time | Description of Weather | Range of $T_A$* | mean $T_A$* |
|---|---|---|---|---|---|
| I | Oct. 29 | 1030 | Clear, warm | 16.3 - 24.4 | 19.3 |
| II | Oct. 29 | 1400 | Overcast, drizzle | 17.8 - 24.9 | 21.3 |
| III | Oct. 30 | 0900 | 2/10 cloud, sunny | 15.4 - 25.5 | 20.9 |
| IV | Oct. 30 | 1200 | 1/10 cloud, hot (sand $T_A$ = 49°C) | 18.3 - 25.5 | 22.5 |
| V | Oct. 31 | 1100 | Overcast (sand $T_A$ = 23.8 °C) | 16.5 - 21.0 | 18.6 |
| VI | Nov. 1 | 0900 | Raining | 12.2 - 15.2 | 13.9 |
| VII | Nov. 1 | 1600 | Overcast, windy Slight clearing 1400 | 14.3 - 16.3 | 15.2 |
| VIII | Nov. 3 | 1900 | Rainy | 13.7 - 18.0 | 14.7 |
| IX | Nov. 4 | 1700 | Rainy | 9.4 - 11.8 | 11.2 |
| X | Nov. 5 | 1130 | Overcast | 10.9 - 15.3 | 13.1 |
| XI | Nov. 5 | 2000 | Clear evening after sunny afternoon | 8.9 - 12.9 | 10.5 |
| XII | Nov. 14 | 1200 | Cloudy, sunny earlier in day | 19.1 - 23.0 | 20.9 |
| XIII | Nov. 23 | 1030 | Clear, sunny (sand $T_A$ = 43.3, air $T_A$ = 25.6 | 21.8 - 26.2 | 24.4 |
| XIV | Dec. 1 | 1800 | Sunny but ~~pen~~ terrarium now shaded | 26.5 - 27.2 | 26.6 |

* $T_A$ of the occupied microhabitats.

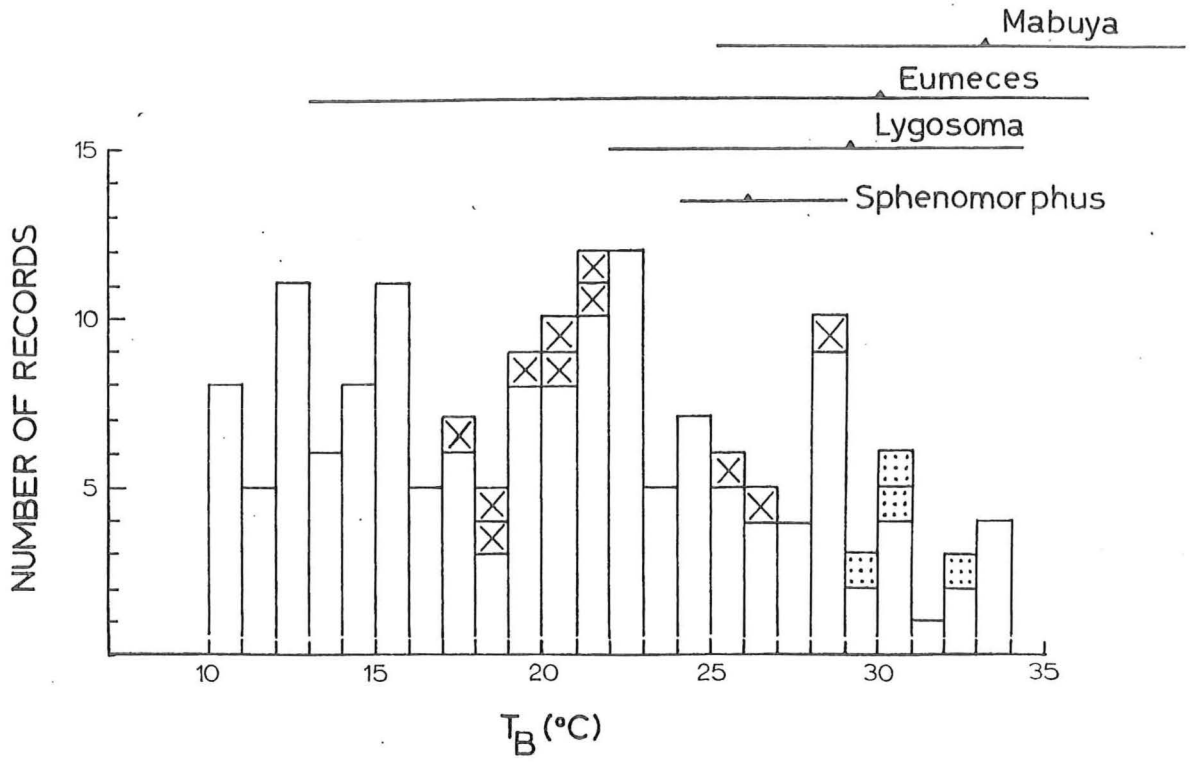

Mabuya
Eumeces
Lygosoma
Sphenomorphus
NUMBER OF RECORDS
15
10
5
10
15
20
25
30
35
$T_B$ (°C)

FIGURE 13

Histogram relating the number of records to the $T_B$ taken in the outdoor terrarium and in the field during the period Oct. 29 to Dec. 1, 1970. Data include $T_B$ used in Figure 10 (dots), 11, and 12, and the $T_B$ obtained at Motunau Island (Nov. 8-11, X's). For comparison, the horizontal lines are the $T_B$ ranges reported in Brattstrom (1965) for four scincid genera. Their mean $T_B$ are indicated by the triangles. They are arranged from the most (top) to the least thermophilic.

reflects recent movement of the skink into the microhabitat in which it was recovered. Because of the rapid cooling and heating of small ectotherms, it would be necessary to shuttle between warmer and cooler microclimates to maintain a differential of more than a few degrees. There is no evidence concerning the efficiency with which small scincids can utilize solar radiation without the added effect of the substrate as a heat source. The few points below the isothermal line ($T_B = T_A$) also indicate movement but from a cooler to the warmer microhabitat in which the skink was recovered (Figure 11). On overcast and even rainy days, skinks were apparently utilizing warmer microclimates, e.g. in the shelter, before recapture. This would suggest that these ectotherms are probably active - locomotory, thermoadjusting, feeding or other activities - under suboptimal macroclimatological conditions. Field evidence is lacking for L. lineoocellatum. The more thermophilic skink, Eumeces fasciatus, has an optimum $T_B$ of 34 °C but its activity is not affected by $T_B$ many degrees lower: pairing still occurs at 21 °C, feeding at 16 °C, and normal locomotion is possible at 10 °C (Mertens, 1960).

When the same data are plotted against the time of day of the temperature recordings (Figure 12) and the macroclimatological data are consulted, the effect of insolation is clear. No more than two sets of recordings were taken on a particular day because of the possibility of adverse stress from multiple recapture, handling, and cloacal recording. With efficient handling, it was felt that daily measurements would not affect their activity. In the period of the study, by 1000 hours some of the skinks had $T_B$ as high as any recorded in the terrarium or in the field. In less than an hour after sunset, the mean $T_B$ had decreased about 20 °C. It appears that these small ectotherms would have to be able to tolerate rapid heating and cooling over a wide range from about 20 degrees in the summer to perhaps 30 °C in winter on clear sunny days. The mean $T_B$ on days when there was sufficient insolation to provide a wide variety of microclimates (Figure 12: I, IV, XIII, and XIV)

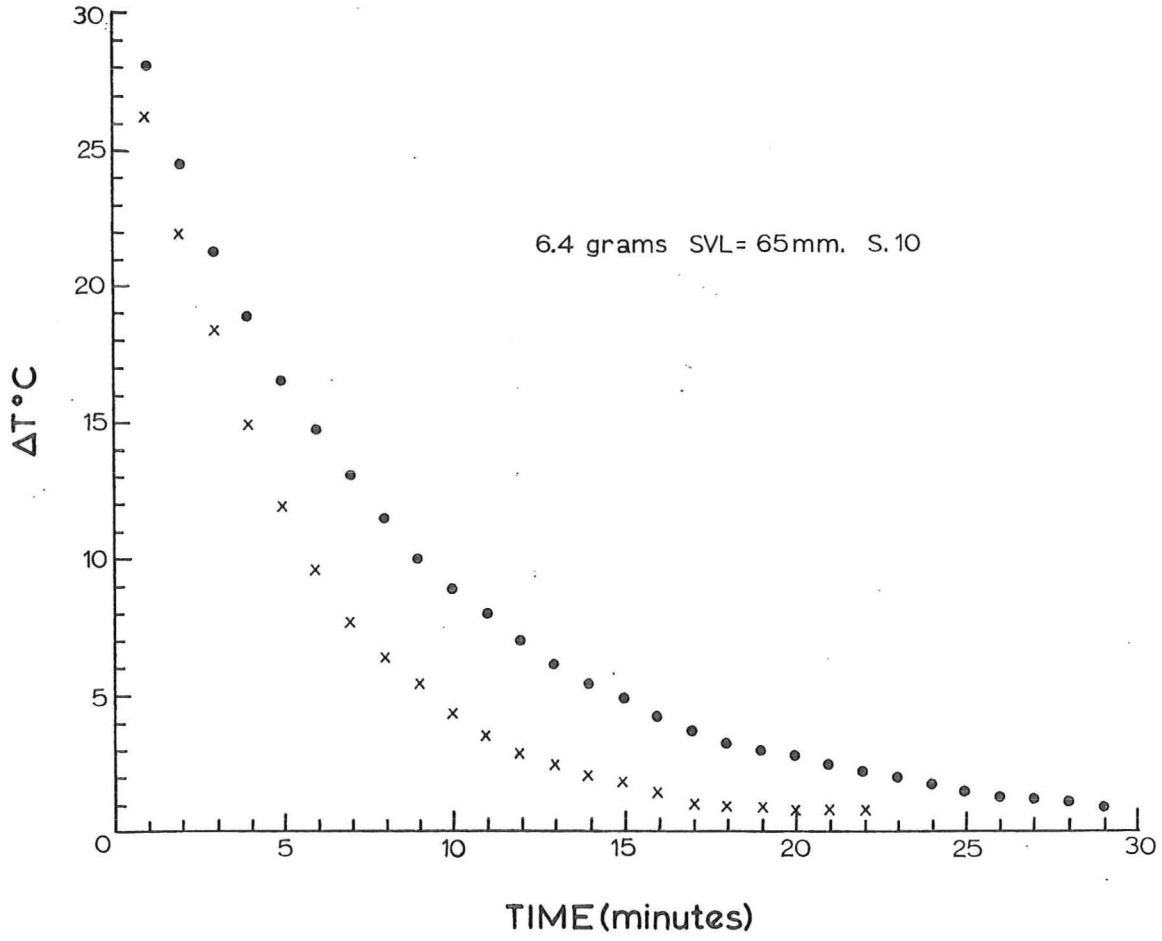

6.4 grams SVL= 65mm. S.10
ΔT°C
TIME (minutes)
0
5
10
15
20
25
30

FIGURE 14

Relation of the difference between $T_B$ and $T_A$ (ie. $\Delta T$) to time. Symbols: ● and X indicate $\Delta T$ for cooling and heating respectively for a live animal. During cooling and heating $T_A$ were 5 °C and 35 °C respectively and $\Delta T$ was 30 °C at time = 0.

was 28.4 °C (range of 19.0 - 33.9 °C). On a clear warm day on July 2, 1970 at 1200 hours, the $T_A$ under pingao was 14.3 and under a log in wet sand the $T_A$ was 11.7 °C. These temperatures were about 10 °C below the $T_A$ recorded four months later. No L. lineoocellatum were found on that day but L. zelandica had a $T_B$ range 24.5 - 28.7 °C (N=4) and one H. pacificus was 14.5 °C. There are a few interesting sequences of recordings in Figure 12. Between I and II, the mean $T_B$ had decreased three degrees whereas the average $T_A$ had increased by two degrees during the four and one-half hour interval between recordings. The weather had become steadily more overcast. The maximum $T_B$ of II was conspicuously affected by the decreased insolation. In III and IV, there was strong insolation; the mean $T_B$ had increased about five degrees whereas the mean $T_A$ had only increased about a degree. Between VI and VII, there had been slight clearing before becoming overcast once again. The mean $T_B$ had increased almost two degrees and the maximum $T_B$ increased three degrees whereas the ranges of $T_A$ had increased only slightly and the mean $T_A$ had increased just over a degree. This would suggest that the skinks had been basking during short periods of insolation.

The daily $T_B$ of L. lineoocellatum obtained from the terrarium and the field over about a month period for a variety of weather conditions are plotted in a histogram (Figure 13). Since no type of weather was favoured for thermometric determinations, it appears that the skinks experience a wide range of daily $T_B$ with a preponderance of $T_B$ below 23 °C (except for the $T_B$ interval 28 - 29 °C). When the $T_B$ ranges of four other genera of scincids are compared with these data, Leiolopisma resembles Eumeces in its range but not its mean $T_B$. Mabuya rudis is the most heliothermic of the scincids. It is known not to become active until the azimuth of the sun has increased permitting it to bask. This lizard is physiologically adapted to a higher range of $T_B$. On the other hand Sphenomorphus sabanus, which is sympatric with M. rudis in Borneo, avoids direct sunlight and open areas when the

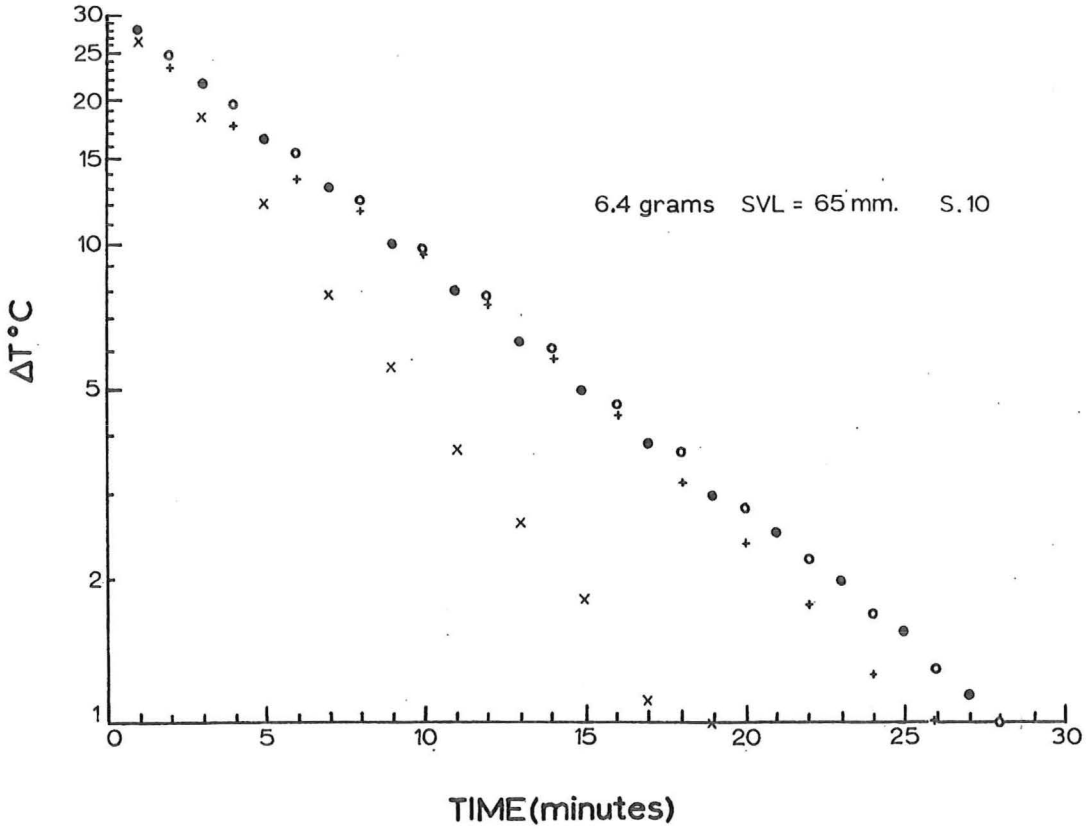

6.4 grams SVL = 65 mm. S.10
ΔT°C
TIME (minutes)
30
25
20
15
10
5
2
1
0
5
10
15
20
25
30

FIGURE 15

Relation of $\Delta T$ plotted logarithmically against time for the same animal when alive (same data as Figure 14) and dead. Symbols: as in Figure 14 with ○ and + indicating cooling and heating of the dead skink respectively.

sun is high. Its restriction to the cooler forest areas suggests that it is adapted to lower $T_B$. Because of their different physiological requirements, these species are considered ecologically isolated in distinct microhabitats or by different activity periods (Inger, 1959). Eumeces obsoletus maintains a $T_B$ slightly above 30 °C when abroad and active (Dawson, 1960). Lygosoma laterale is active throughout much of the year although it is not significantly active during December and January coincident with cool weather and overcast days (Hudson and Bertram, 1966). Both of these species occur in the central U.S.A. The adults of E. obsoletus weigh over 20 grams, L. laterale are under 2 grams whereas L. lineoocellatum individuals used in this study were intermediate weighing 3 - 13 grams*. The size of an ectotherm is important when comparing its thermal relations because of the effect of size on rates of heating and cooling. The mean $T_B$ for L. lineoocellatum under optimal conditions 28.4 °C, with a maximum of 33.9 °C. Leiolopisma fucum and L. rhomboidalis were reported to have mean $T_B$ of 30.8 and 28.9 °C with maximum $T_B$ of 34.5 and 35.0 °C respectively (Wilhoft, 1961). Studies on the thermal relations of other scincids, particularly Leiolopisma species, are lacking.

L. lineoocellatum, like other scincids studied, does not have a 'preferred' $T_B$ but it appears to be capable of activity over a wide range of $T_B$. Although there is some evidence that they bask, it is not conspicuously heliothermic like most iguanids for example. Even on days when the substrate $T_A$ were above 45 °C, no skink was found to have a $T_B$ above 34 °C. Since many vertebrates have been shown to maintain $T_B$ (endogenously or exogenously) near their lethal limits, L. lineoocellatum because of its relatively small size would have a very small margin of safety against heat death. This would make a precise temperature sense and control

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* Specimens weighing up to 23 grams have since been found near the baches.

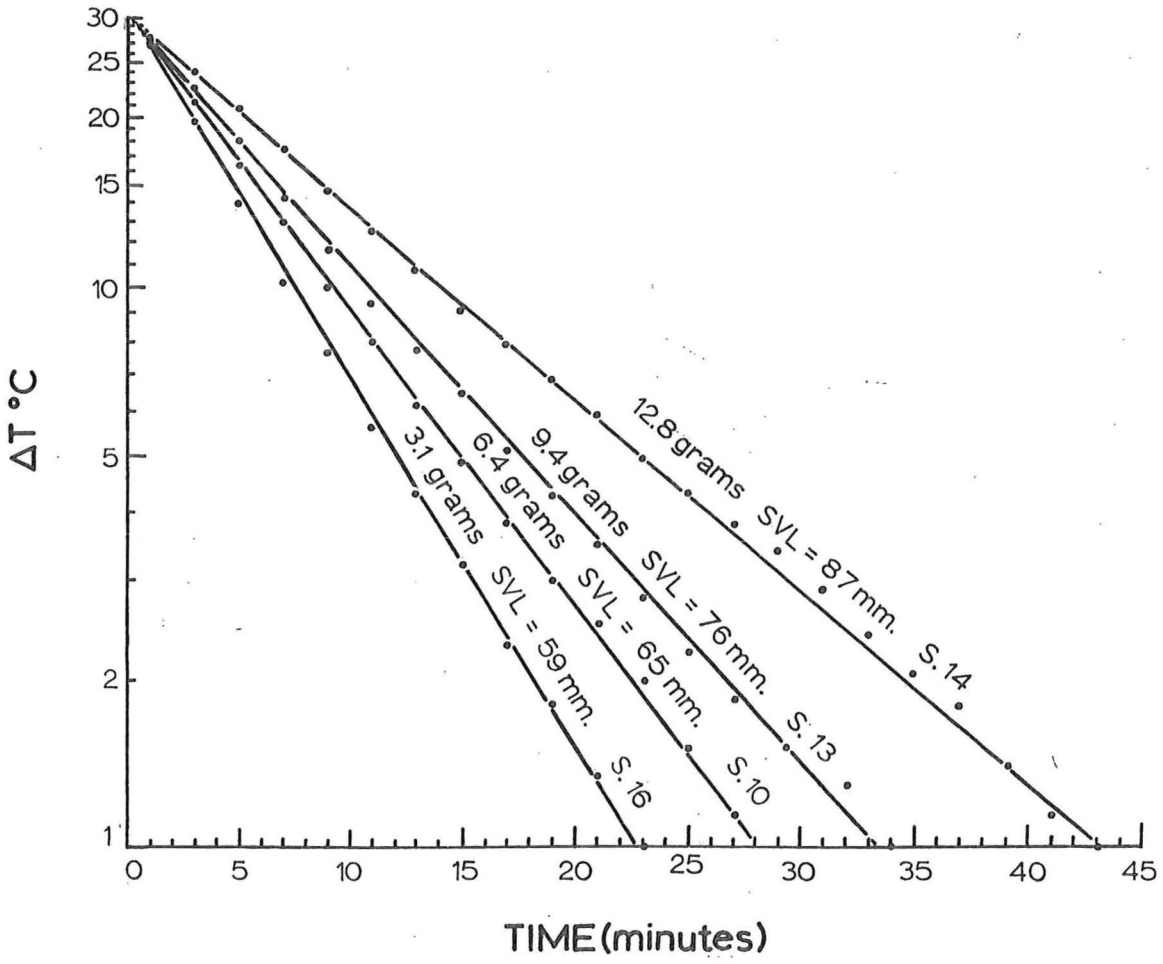

30
25
20
15
10
5
2
1
ΔT °C
0
5
10
15
20
25
30
35
40
45
TIME (minutes)
12.8 grams SVL = 87 mm. S. 14
9.4 grams SVL = 76 mm. S. 13
6.4 grams SVL = 65 mm. S. 10
3.1 grams SVL = 59 mm. S. 16

FIGURE 16

Relation of $\Delta T$ to time for skinks of different weights and sizes (Snout-Vent Lengths) plotted semilogarithmically. The lines are fitted by eye and intercept the abscissa at the time taken to cool to within one degree of the $T_A$ (log $\Delta T = 0$)

(shuttling between sun and shade) almost mandatory. Nothing is known, however, about reptilian thermophysiological control sites other than that there is no evidence for hypothalamic involvement (Templeton, 1970). Because of the rapid heat exchange of small bodies it is unlikely that the simple off-on control using exogenous heat sources would be sufficient to maintain a constant $T_B$ without large oscillations, regardless of the precision of their internal set points. Small endotherms maintain their $T_B$ at the price of an extravagant metabolic rate. Because of the thermodynamic problems involved, small ectotherms would probably avoid direct insolation unless the substrate were cool (in which case it would be a useful heat sink). The secretive habits of most scincids may be due, in part, to their avoidance of high $T_A$ and intense insolation. But their small size has its advantages since - assuming that they have a well developed temperature sense - they can select suitable microclimates in and under vegetation and avoid predation as well.

Since most lizards would avoid reaching their lethal limits of $T_B$, their heat resistance may merely be a by-product of their physiological adaptations to their $T_B$ range when active. As a general rule, iguanids, agamids, and teiids are the most heat resistant while scincids, anguids, and xantusids are not heat resistant, and gekkonids occur in both groups. At the other end of the biothermal scale, most lizards avoid freezing by burrowing. Heat resistant forms are also cold sensitive (for reasons which will be discussed below) and therefore they brumate during cold periods to avoid cold narcosis. Cold resistant forms, however, may continue to be active under conditions of sufficient insolation to bask or they may become cold torpid. Torpidity is a state of inactivity and low $T_B$ which is not accompanied by the physiological temperature - independent changes characteristic of brumation. Because of the mild winter (1970), it was not possible to determine whether Leiolopisma species are active on very cold sunny days. Nevertheless, they are not known to brumate.

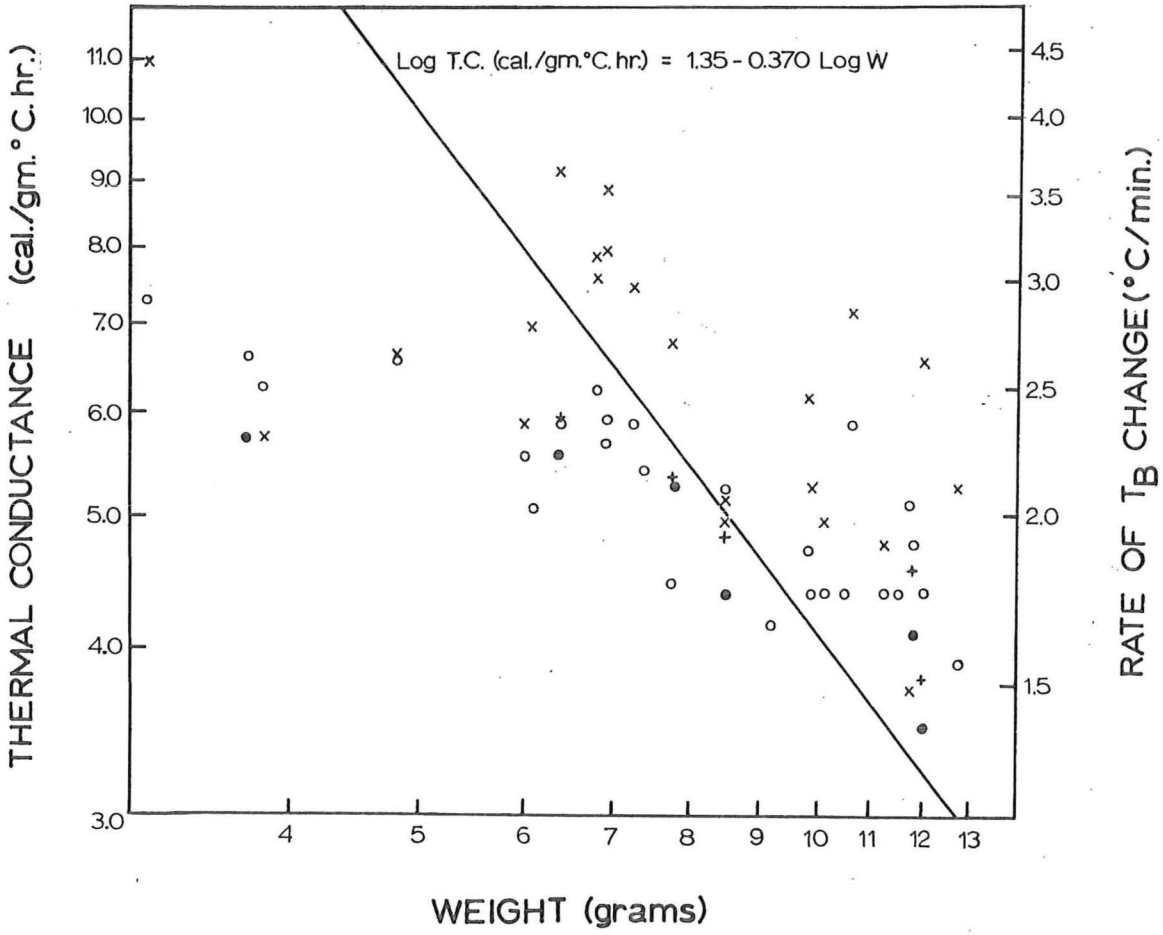

Log T.C. (cal./gm.°C.hr.) = 1.35 - 0.370 Log W
THERMAL CONDUCTANCE (cal./gm.°C.hr.)
RATE OF $T_B$ CHANGE (°C/min.)
WEIGHT (grams)
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
4
5
6
7
8
9
10
11
12
13

FIGURE 17

Relation of Thermal Conductance and Rate of $T_B$ change to weight at 20 °C ( $\Delta T = 15$ °C). Symbols as in Figure 15. For comparison, the line and equation determined by Bartholomew and Tucker (1964) for a higher and wider range of body weights at 30 °C ( $\Delta T = 10$ °C) is given.

## B. HEATING AND COOLING

### 1. Thermal Properties

#### a. Specific Heat (S.H.)

The average for ten skinks was 0.79 calories/gram/ $^{o}$C (range, 0.74 - 0.85). Other authors have assumed a value of 0.82 but they have not indicated how the value was obtained (Bartholomew and Tucker, 1964). Lizards are similar to mammals regarding this physical property. Frogs were found to have S.H. 0.94 - 0.99 (mean, 0.97) (Fromm, 1956). It is the high water content of these organisms that produces their high S.H. values. The lower the S.H., the less heat is necessary to raise an ectotherms $T_B$ exogenously.

#### b. Thermal Conductance (T.C.)

Eighteen skinks were used for heating and cooling experiments; of these six were sacrificed and heated and cooled as dead subjects. They ranged from 3.7 - 12.8 grams. ECG were obtained simultaneously for nine skinks.

Since the rate at which a body exchanges heat is proportional to the temperature differential (dT), the rate is greatest when dT is greatest (in this case, 30 $^{o}$C) and becomes slow (ie. the curve is almost level) as dT approaches zero degrees (Figure 14). When the same data are plotted semilogarithmically, a straight line is obtained (Figure 15). The rate of cooling for a live and dead skink and the rate of heating for a dead skink were similar. Although in the example given (Figures 14, 15), the rate of heating for a live skink was conspicuously greater, it was felt that this was due to the procedure of heating in the waterbath (where the components of heat transfer were different). In the last six heating trials, the skinks were heated in the temperature cabinet. For these subjects, the rate of heating occurred at the same rate as for cooling, or at only a slightly greater rate. Since these small ectotherms have little insulation and a large surface area-mass ratio, heat transfer is so rapid that cardiovascular and other physiological adjustments

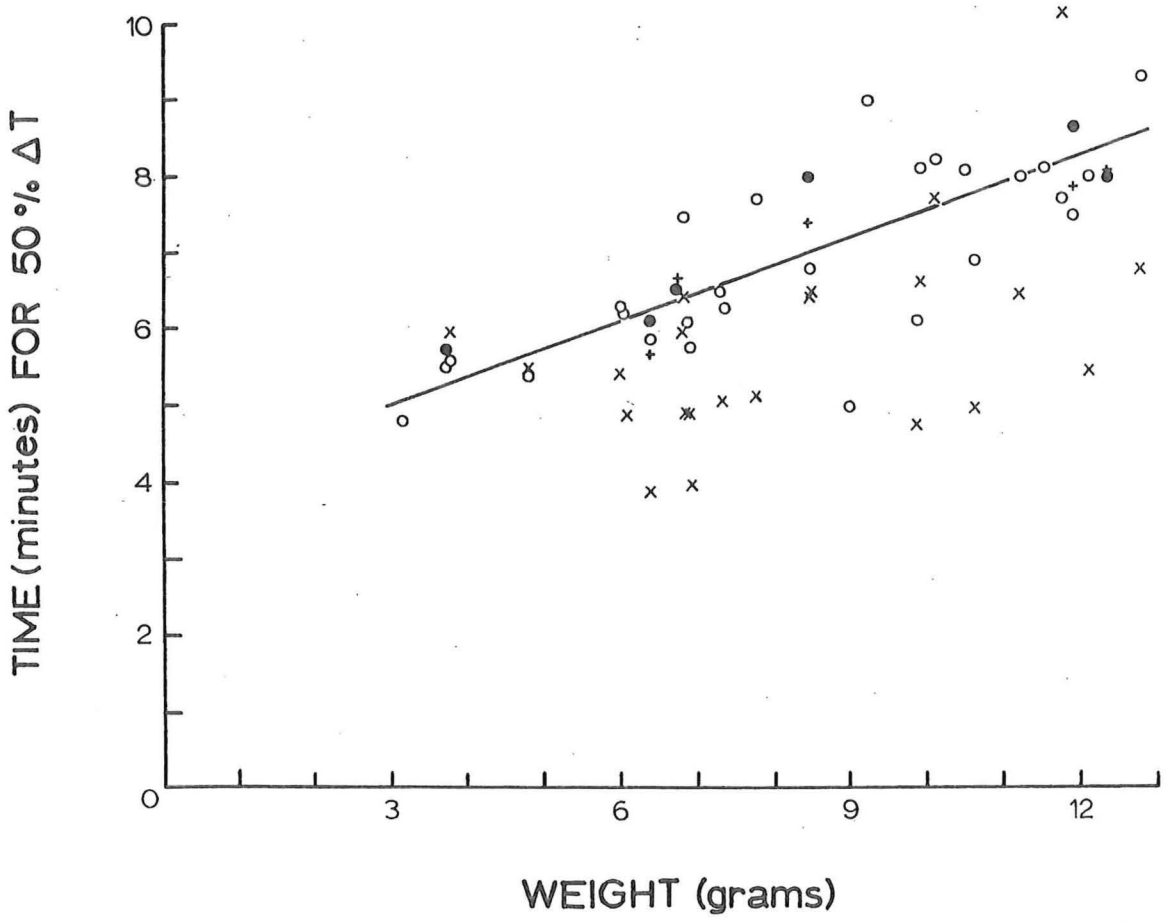

TIME (minutes) FOR 50 % ΔT
10
8
6
4
2
0
3
6
9
12
WEIGHT (grams)

FIGURE 18

Relation of the time taken for 50% of heat exchange ( $\Delta T$) to body weight. Same symbols as in Figure 15. The line fitted by eye is for cooling values for live skink only ( ○ ).

would play a minor role in heat transfer. The larger the skink, the slower it cools (Figure 16). These cooling rates are very nearly linear when plotted semilogarithmically, indicating that small ectotherms cool according to physical principles for inanimate bodies (Newton's Law of Cooling). A simple and convenient method of characterizing the rates of heating and cooling is to determine the rate of heat exchange at 20 °C (when dT = 15 °C). Using the value specific heat/log e and the slope of the curve at 20 °C (Figure 15), it is possible to calculate the thermal conductance as described on page 16. The slope is the rate of change of $T_B$ ($dT_B/dt$) in °C/minute. When the thermal conductance in calories/gram °C is plotted on a log-log graph against the weight, a scatter plot is produced (Figure 17). But the values, particularly for cooling, appear to lie close to a line determined by Bartholomew and Tucker (1964) for four varanid species (16-4400 grams) at 30 °C. For weights less than six grams, the thermal conductance diverges significantly from Bartholomew and Tucker's line.

When the time taken for a skink to heat or cool 15 °C or 50% of their initial dT of 30 °C is plotted against its weight, a line can be fitted to the points for cooling of live skinks (Figure 18). With a greater than four-fold increase in weight, there is a less than two-fold increase in the time taken for cooling 50% of the initial dT. Thus, for the wide range of weights of L. lineoocellatum, there is a difference of less than four minutes in the times taken for cooling 50% of the dT. For small ectothermic species, individuals of different ages (therefore of different sizes) would not have significantly different rates of heat exchange. Between small and large ectothermic species, however, the difference in rates of heat exchange would be considerable. A varanid about 100 times heavier than an average N. Z. skink would take 25 minutes to cool 50% of a dT of about 30 °C (Bartholomew and Tucker, 1964). L. lineoocellatum, by comparison, would take about 7 minutes. Such a difference in heat exchange rates has ecological significance. The rate of temperature change reflects the potential facility of

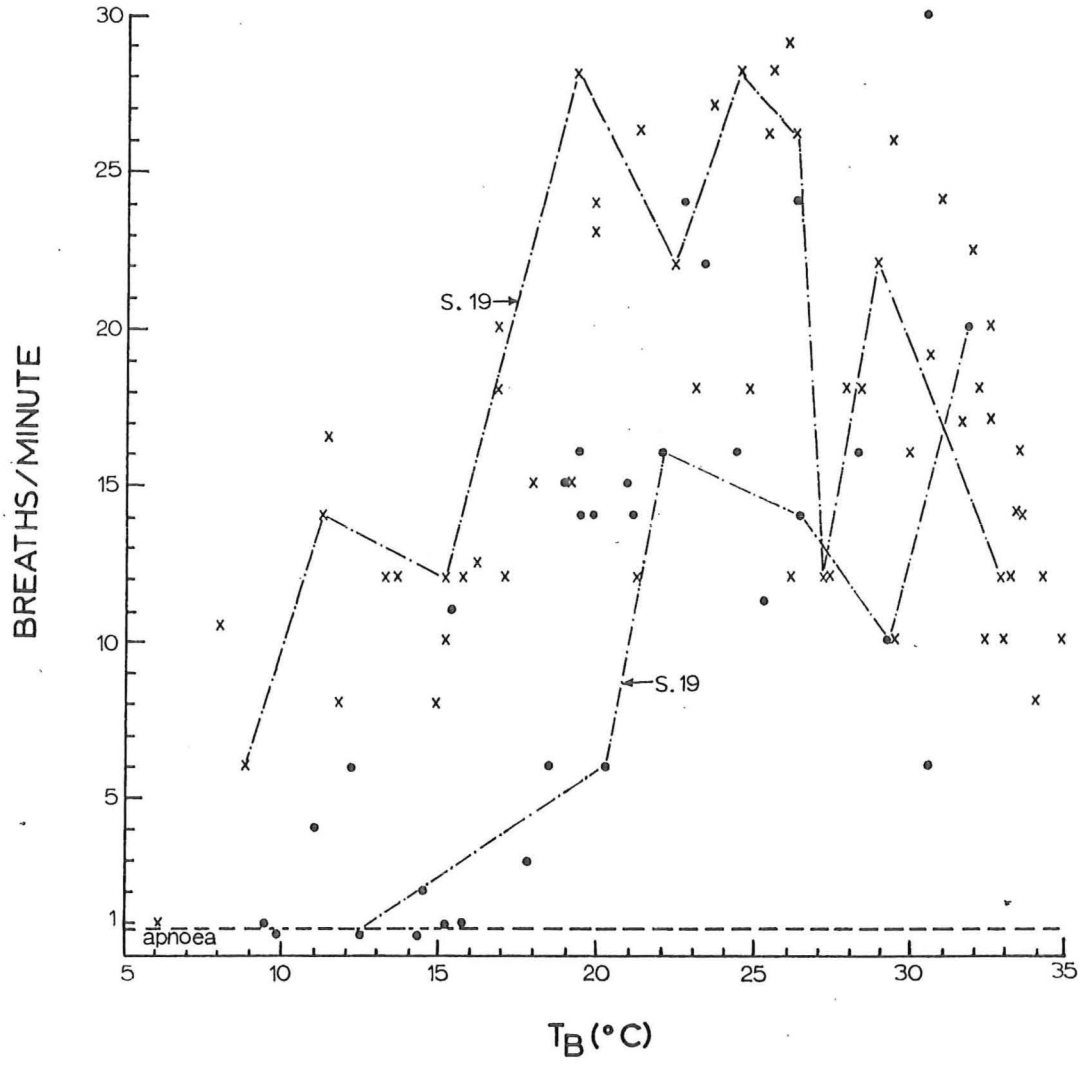

BREATHS/MINUTE
30
25
20
15
10
5
1
S. 19
S. 19
apnoea
5
10
15
20
25
30
35
$T_B$ (°C)

FIGURE 19

Relation of breathing rate to $T_B$ during heating and cooling. Same symbols as in Figure 15. The data for one individual (S.19) are joined by dash-dot lines. The horizontal line arbitrarily represents the upper limit of apnoea (ie. no breaths in a one minute period).

behavioural thermoregulation. The precision of using off-on temperature regulation (shuttling from shade to sun) would be enhanced by a greater mass.

2. Physiological Rate-Temperature Responses to Heating and Cooling

a. Ventilation Rate (V.R.)

Breathing was irregular during heating and cooling (Figure 19). When the rates are plotted against $T_B$, a scatter plot results. The points from records for a typical subject were joined to illustrate the differential effect of heating versus cooling on the V.R. Considering that most skinks took about five minutes for heating 50% of the dT (Figure 18) and a further 15-20 minutes for heating 96% of the dT (where the final dT = 1.0 °C), the heated skinks were breathing 10-30 breaths during most of the heating period; whereas during the cooling experiments, the skinks were breathing less than 10 breaths/minute and often less than one in a minute below 15 °C. Since the V.R. was determined on a per minute basis, a rate of less than one/minute was arbitrarly considered as apnoea. When these skinks did breathe, it was often a few breaths in succession followed by a period of apnoea. In spite of the substantial difference between the V.R. of heated and cooled skinks, the greater V.R. during heating probably did not affect the rate of heat exchange. The lungs are very small in L. lineoocellatum relative to their total mass and the tidal volume would also be small.

b. Heart Rate (H.R.)

When the H.R. was plotted semilogarithmically against the $T_B$ during heating and cooling, no difference was apparent between their rate-temperature curves except perhaps below 15 °C (Figure 20). Considering that it took only a few minutes to reach 15 °C during heating, the slightly increased H.R. would have had very little effect in heat transport. Since cardiac output is equal to the stroke volume times the H.R., if the stroke volume had remained unchanged, there would have been a slight increase in the cardiac output. The H.R.-$T_B$ response during heating and cooling was above

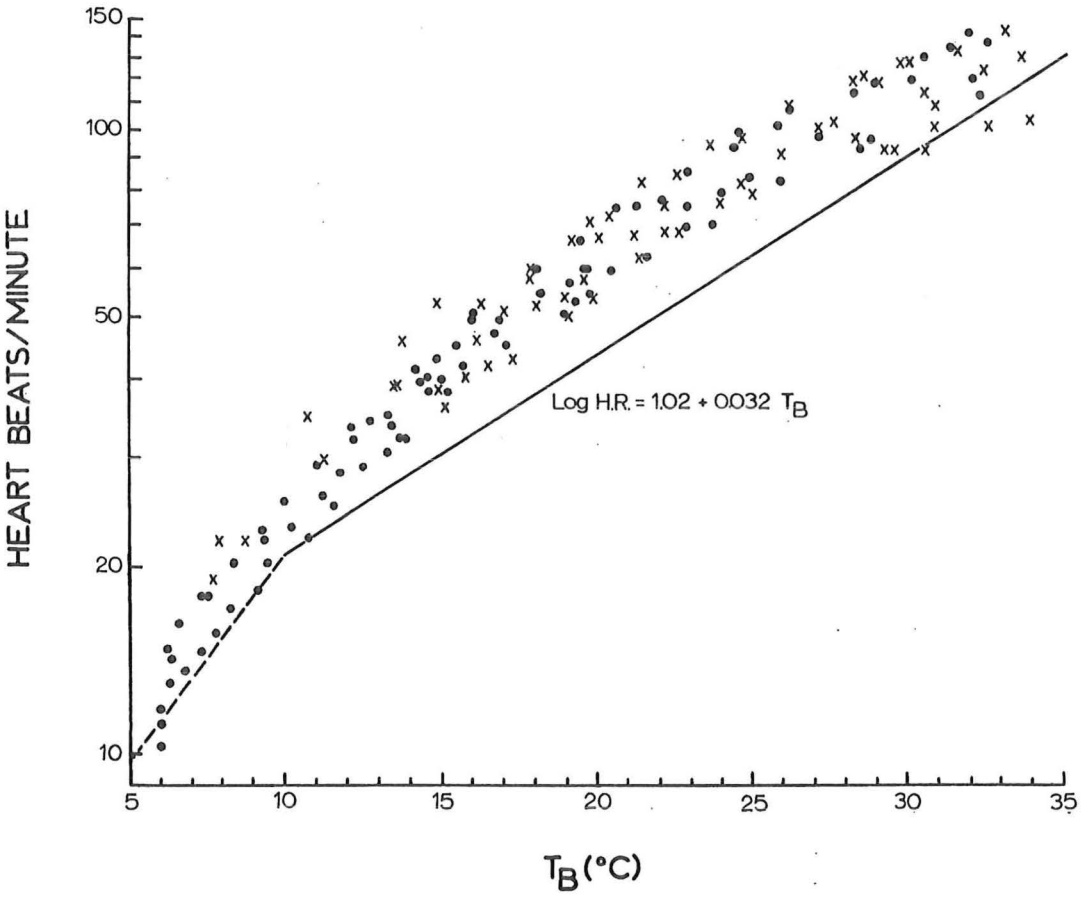

HEART BEATS/MINUTE
150
100
50
20
10
5
10
15
20
25
30
35
Log H.R. = 1.02 + 0.032 $T_B$
$T_B$ (°C)

FIGURE 20

Relation of heart rate to $T_B$ during cooling and heating. Symbols as in Figure 15. For comparison, the line determined for resting skinks at equilibrated temperatures (Figure 32) is included.

the line determined for resting skinks at equilibrated temperatures over the interval 13-28 °C (Figure 32). This suggests that the skinks were under stress during the period of rapid heat exchange. The resultant cardioacceleration was probably due to the activity of the sympathetic nervous system.

c. Analyses of the Cardiac Cycle

The durations of various cardiac events were graphed semilogarithmically against $T_B$ during cooling to determine which intervals were most affected by the rapid cooling (Figure 21). A useful approximation of a rate-temperature response is the temperature coefficient $Q_{10}$. If the rates $K_1$ and $K_2$ at any $T_B$ ($T_1$ and $T_2$) are known, then the $Q_{10}$ is equal to the ratio of these rates raised to the power $10/T_1 - T_2$, or

$$\log Q_{10} = \frac{10 (\log K_1 - \log K_2)}{T_1 - T_2}$$

Since the slope of a line on a semilog graph is determined by the equation

$$\text{slope} = \frac{\log K_1 - \log K_2}{T_1 - T_2}$$

then, the logarithm of $Q_{10}$ is equal to ten times the slope or

$$Q_{10} = \text{antilog } (10 \times \text{slope})$$

In this way, a $Q_{10}$ can be determined from the equation of a line of best fit on a rate-temperature semilogarithmic plot. According to van't Hoff's rule, the $Q_{10}$ of chemical reactions lie between 2 and 3, whereas the physical changes often have higher or lower $Q_{10}$ values. Over the narrow biological range of temperatures, the $Q_{10}$ approximation and the Arrhenius constant $\mu$ vary practically in the same manner. Since the $Q_{10}$ is easier to apply and since neither coefficient can extend beyond a purely descriptive means of presenting data (Scholander, Flagg, Walters, and Irving, 1955), the $Q_{10}$ was used to characterize all rate-temperature responses.

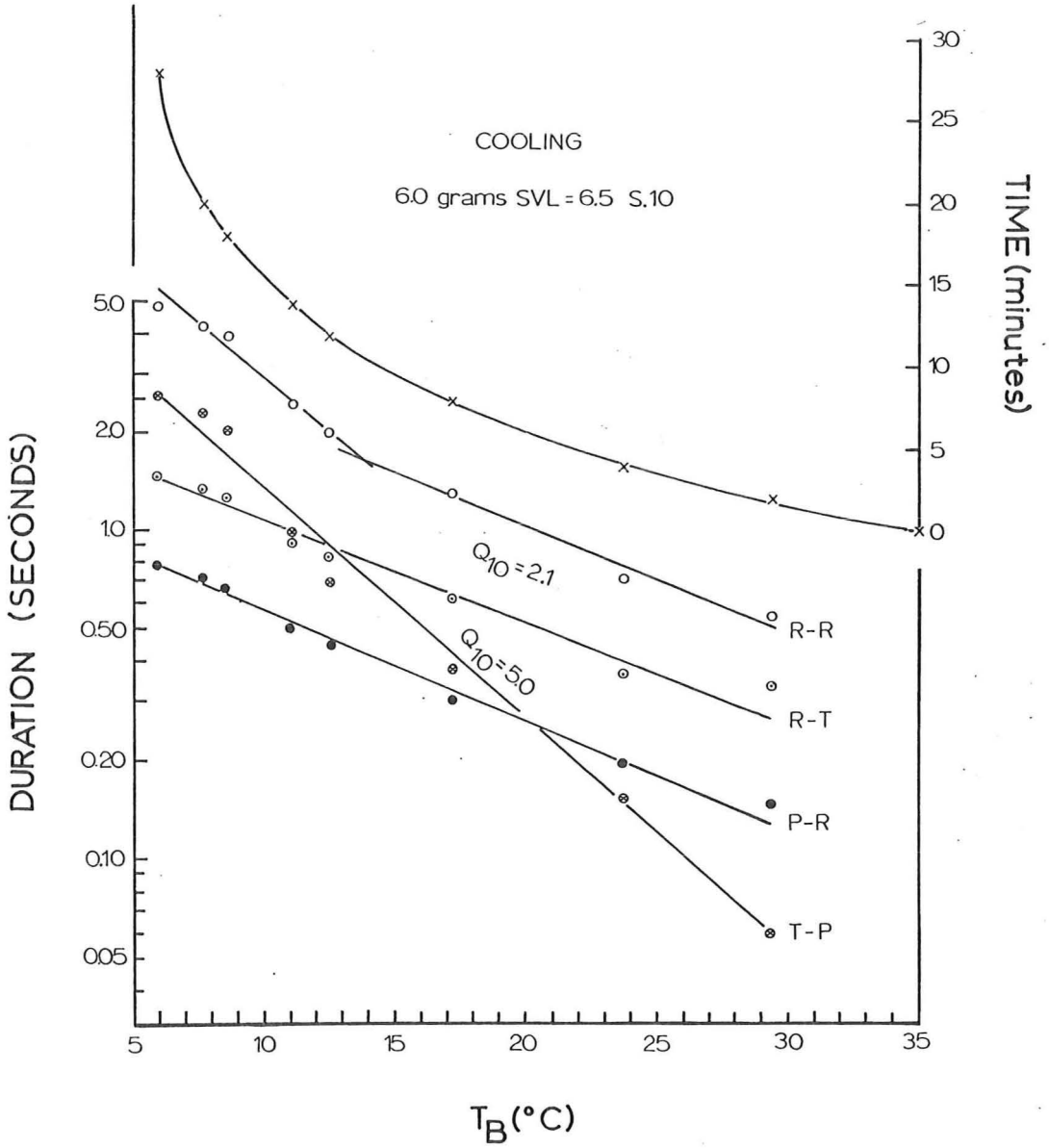

COOLING
6.0 grams SVL = 6.5 S.10
DURATION (SECONDS)
TIME (minutes)
$T_B$(°C)
$Q_{10}$ = 2.1
$Q_{10}$ = 5.0
R-R
R-T
P-R
T-P
5.0
2.0
1.0
0.50
0.20
0.10
0.05
30
25
20
15
10
5
0
5
10
15
20
25
30
35

FIGURE 21

Relation of the durations of the P-$R_1$, R-$T_1$, T-P and R-R intervals to $T_B$ for the cooling of one individual (S. 10). All lines are fitted by eye. The $Q_{10}$ values are for the reciprocals of the intervals and have been included to characterize the relative slopes of the lines. Relation between time and $T_B$ (cooling curve) is plotted for each series of intervals ($\overline{X}-X$). Other symbols are self-explanatory. Compare these date with Figures 33 and 34.

The effect of the T-P interval in stretching the duration of the R-R interval as the skink is cooled below 15 °C is illustrated (Figure 21). The $Q_{10}$ values for the reciprocals of the P-R, R-T, and R-R intervals do not differ substantially from the values for the same intervals for skinks at $T_{EQ}$. (Figures 33, 34), but the durations of these intervals determined during a cooling experiment were conspicuously shorter (especially at the lower $T_B$) when data from the same subject are compared. (Table V).

TABLE V : A comparison of durations of intervals (in seconds and heart rates for cooling and equilibration experiments for the same skink (S. 14).

| $T_B$ (°C) | 20 | | 10 | | 6 | |
|---|---|---|---|---|---|---|
| Intervals | Cooling | Equil. | Cooling | Equil. | Cooling | Equil. |
| P-R | 0.25 | 0.32 | 0.52 | 0.92 | 0.8 | 1.30 |
| R-T | 0.50 | 0.60 | 0.92 | 1.81 | 1.5 | 2.52 |
| T-P | 0.27 | 0.64 | 1.02 | 1.39 | 2.6 | 3.40 |
| R-R | 1.02 | 1.56 | 2.46 | 4.12 | 4.9 | 7.22 |
| Heart Rates (beats/minute) | 59.0 | 38.5 | 24.5 | 14.6 | 12.2 | 8.3 |
| % difference | 65 | | 60 | | 68 | |

C. EQUILIBRATION EXPERIMENTS

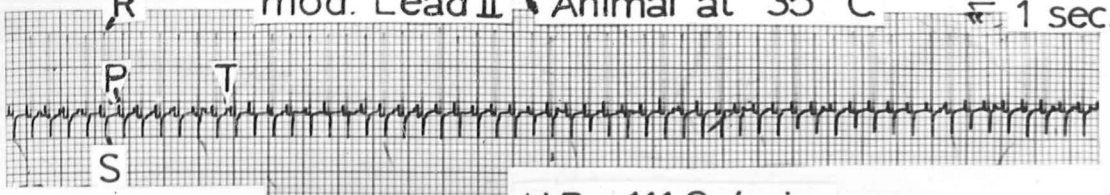
When the $T_A$ is changed in order to determine some rates at different $T_B$, it is ordinarily assumed that under the conditions of equilibration of the temperatures ($T_B = T_A$ or $T_{EQ}$) the rates are not seriously affected by the speed of temperature change or

1 minute after commencement of cooling trial

JAN. 2, 1971 12.8 grams { Refrigerator at 5° C. / Animal at 35° C

mod. Lead II

130 μV 1 sec.

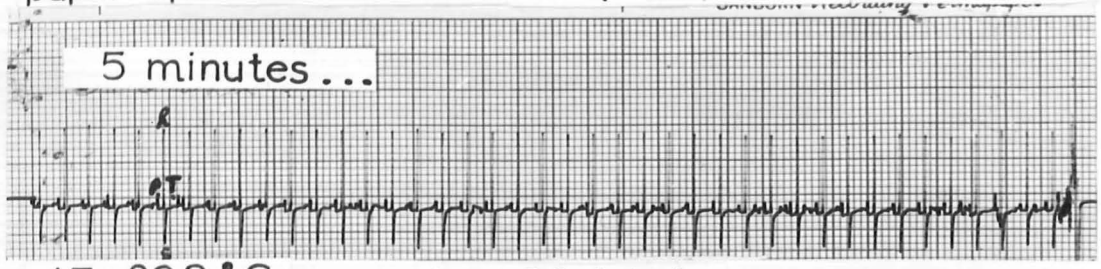



ΔT = 28.3° C. H.R. = 111.0 /min.

1000x preamplification and x5 attenuation

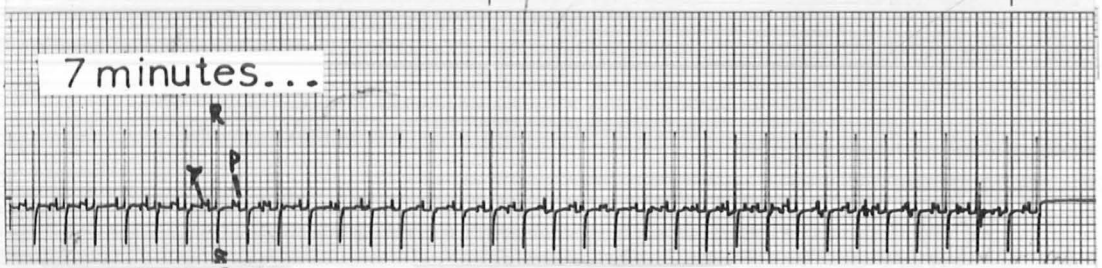
paper speed = 5 mm./sec. Freq. Response = 8 ~ - 50 ~

5 minutes ...



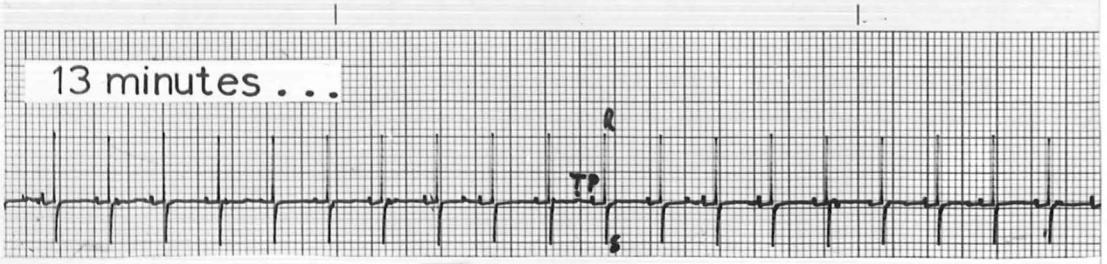

ΔT = 20.8° C. H.R. = 82.4 /min.

7 minutes...



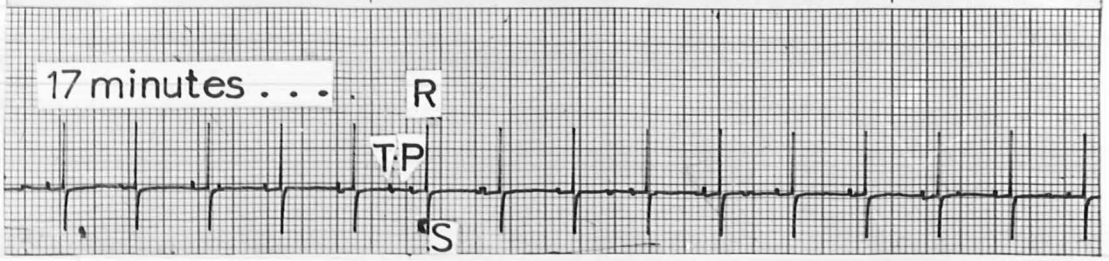

ΔT = 17.8° C. H.R. = 68.3 /min.

13 minutes ...




ΔT = 10.6° C. H.R. = 37.6 /min.

17 minutes ...




ΔT = 8° C. H.R. = 28.5/min.

N.B. Cooling trial continues on following page

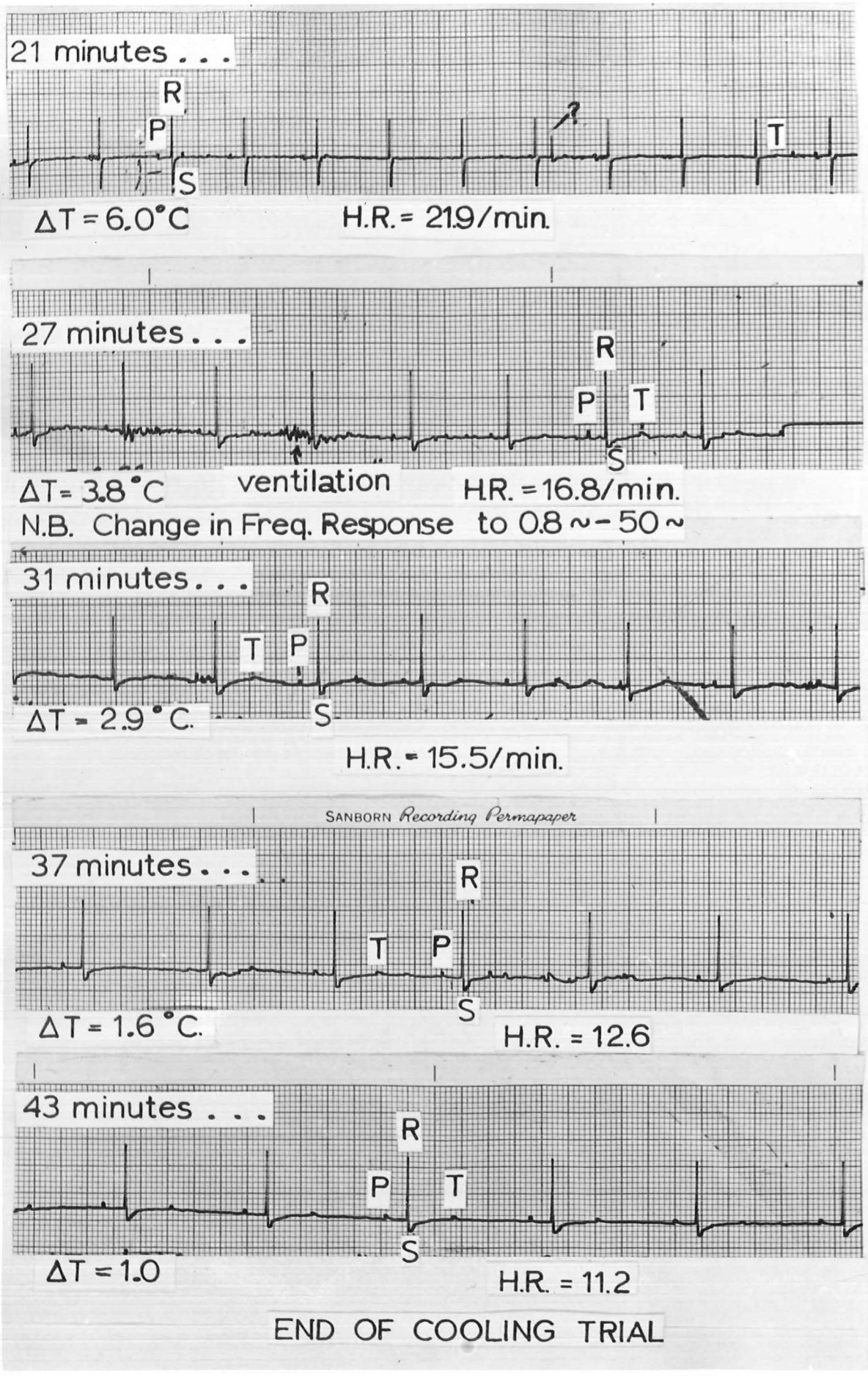

21 minutes . . .
R
P
S
T
ΔT = 6.0°C
H.R. = 21.9/min.
27 minutes . . .
R
P
T
S
ventilation
ΔT = 3.8°C
H.R. = 16.8/min.
N.B. Change in Freq. Response to 0.8 ~ - 50 ~
31 minutes . . .
R
T
P
S
ΔT = 2.9°C.
H.R. = 15.5/min.
SANBORN Recording Permapaper
37 minutes . . .
R
T
P
S
ΔT = 1.6°C.
H.R. = 12.6
43 minutes . . .
R
P
T
S
ΔT = 1.0
H.R. = 11.2
END OF COOLING TRIAL

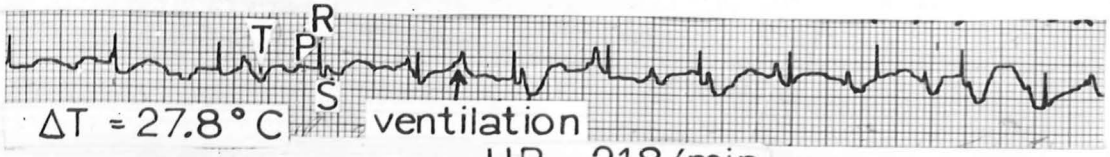
FIGURE 22

Typical ECG for one individual (S. 14) taken at various times during a cooling experiment.

1 minute after commencement of heating trial

S. 14 JAN. 2, 1971. { Refrigerator at 35 °C.
Animal at 5° C.

260 μV
1 sec.

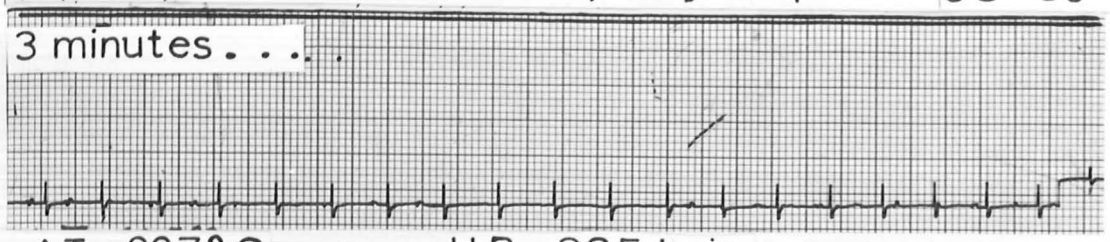



ΔT = 27.8 °C ventilation

H.R. = 21.8/min.

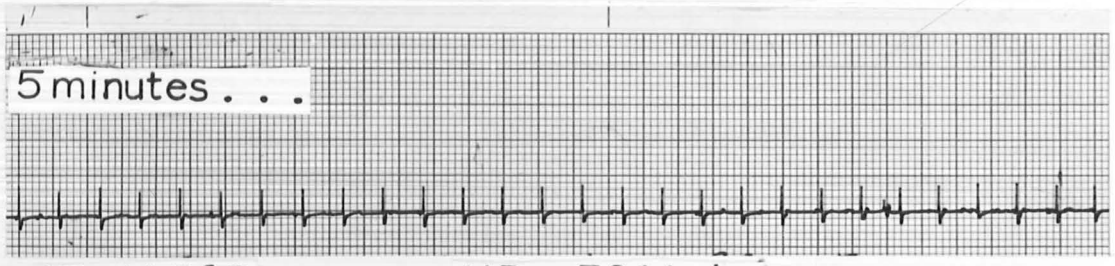
1000x preamplification & x10 attenuation

paper speed = 5 mm./sec. Frequency response = 0.8 - 50 ~

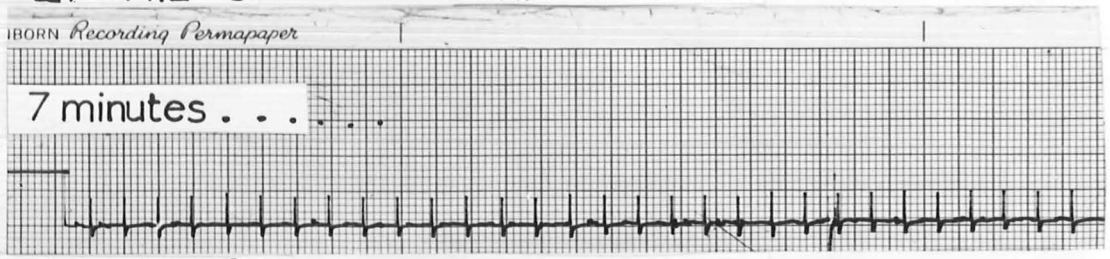



ΔT = 22.7° C. H.R. = 38.5/min.

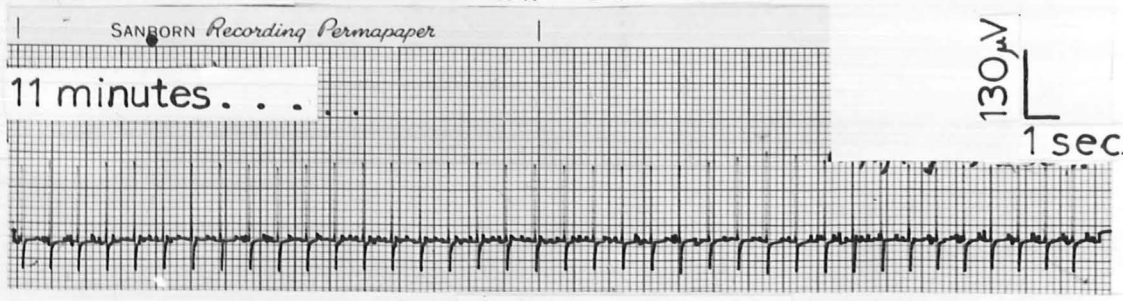
N.B. Change in freq. response to 8 - 50 ~




ΔT = 14.2 °C. H.R. = 52.1/min.




ΔT = 17.8 °C. H.R. = 61.6/min.




130 μV
1 sec.

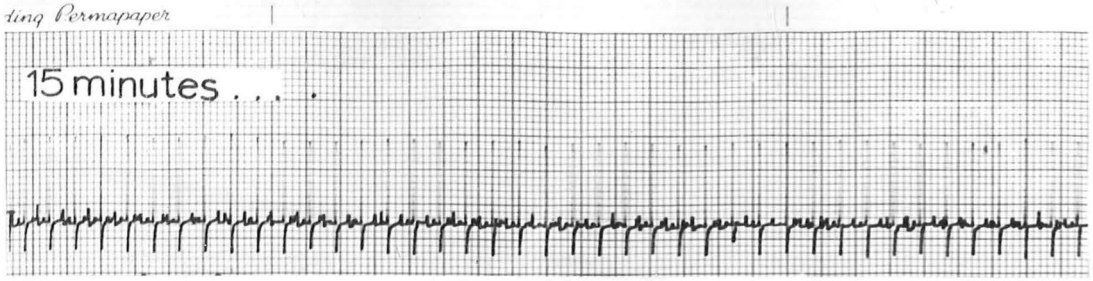
ΔT = 10.2 H.R. = 73.5/min.

N.B. Change in attenuation to x5

Heating trial continues on following page

ting Permapaper

15 minutes . . . .



ΔT = 8.2 °C. H.R. = 73.2

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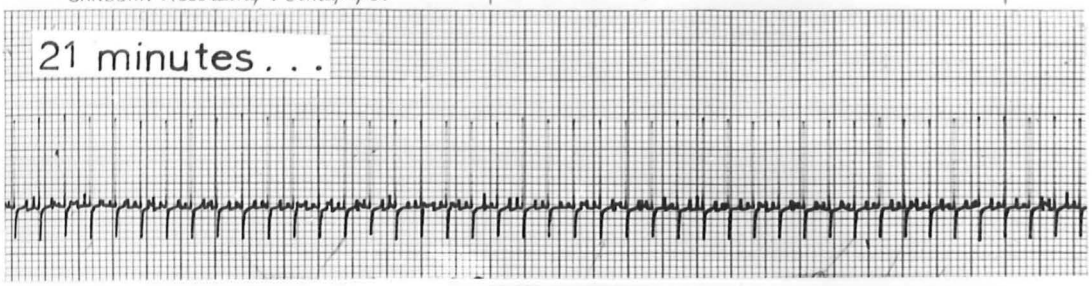
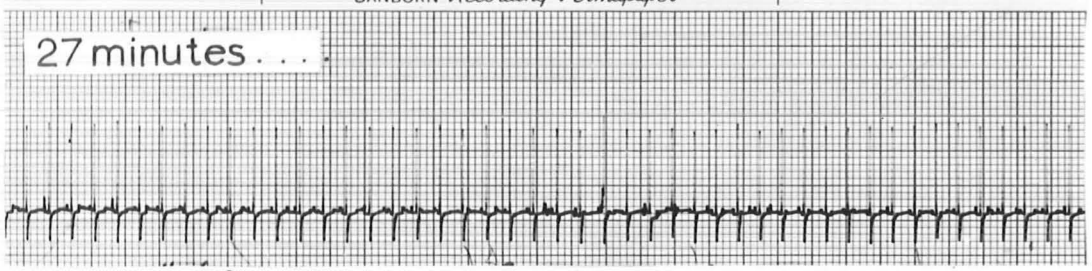
21 minutes . . .



ΔT = 7.0 °C. H.R. = 80.9

SANBORN Recording Permapaper

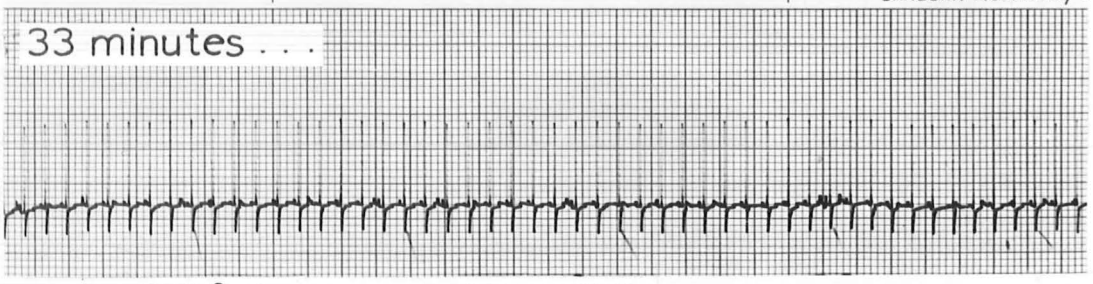
27 minutes . . .



ΔT = 4.6 °C. H.R. = 90.6

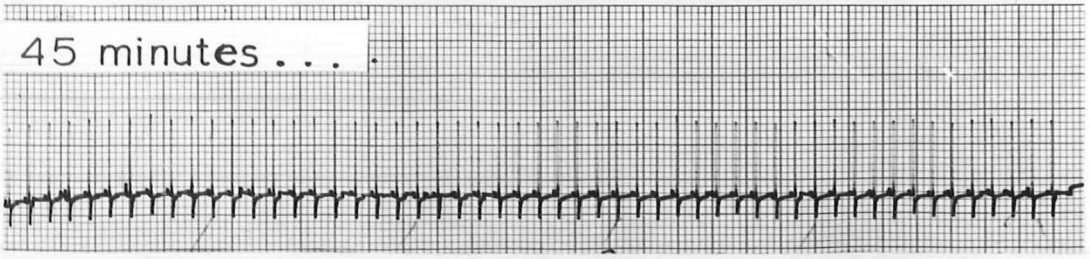
SANBORN Recording

33 minutes . . .



ΔT = 2.9 °C. H.R. = 97.2

45 minutes . . .



ΔT = 1.1 °C. H.R. = 102.3

END OF HEATING TRIAL

FIGURE 23

Typical ECG for one individual (S. 14) taken at various times during the subsequent heating experiment.

the length of time spent at the new $T_{EQ}$. To standardize the conditions in these experiments, the skinks were equilibrated for a minimum of an hour, and longer periods when the experimental $T_A$ was changed 10 °C or more at a time. For EOG experiments, the skinks were brought to 0 °C and held for a few hours until a clear tracing had been obtained, then the $T_A$ was raised in 5 °C steps - equilibrating at least an hour - up to 35 °C.

Although physiological responses were measured over the $T_B$ 0-35 °C, the emphasis was directed to low $T_B$. The physiological capacity of an organism at certain $T_B$ is reflected by measures of metabolic, ventilation, and heart rates which are interrelated physiological processes.

1. Standard Metabolic Rate (S.M.R.)

Fifteen skinks were used to determine the rates of oxygen consumption at various $T_B$ over the range 5 - 35 °C. Their weights ranged from 3.3 - 13.0 grams. All subjects were fasted for at least three days before the experimental period and during it, but water was always available between experiments. When the skinks were released into a container in the laboratory after a series of determinations (especially for those above room temperature), some animals were seen lapping up water, others submerged their heads and occasionally their whole bodies. Their weights usually decreased during the experimental period, but there were significant increases as well (Figure 24) which could only have been due to water consumption. Two of the three skinks which had food available for nine days between periods of experimentation had gained weight (S. 14 and S. 7).

The relation of the mean S.M.R. to $T_B$ when plotted semilogarithmically was linear over the $T_B$ range 5 - 35 °C (Figure 25). The equation of the line fitted by eye is,

$$\log O_2 \text{ consumption (mean)} = (8.28 - 10) \mp 0.035\ T_B$$

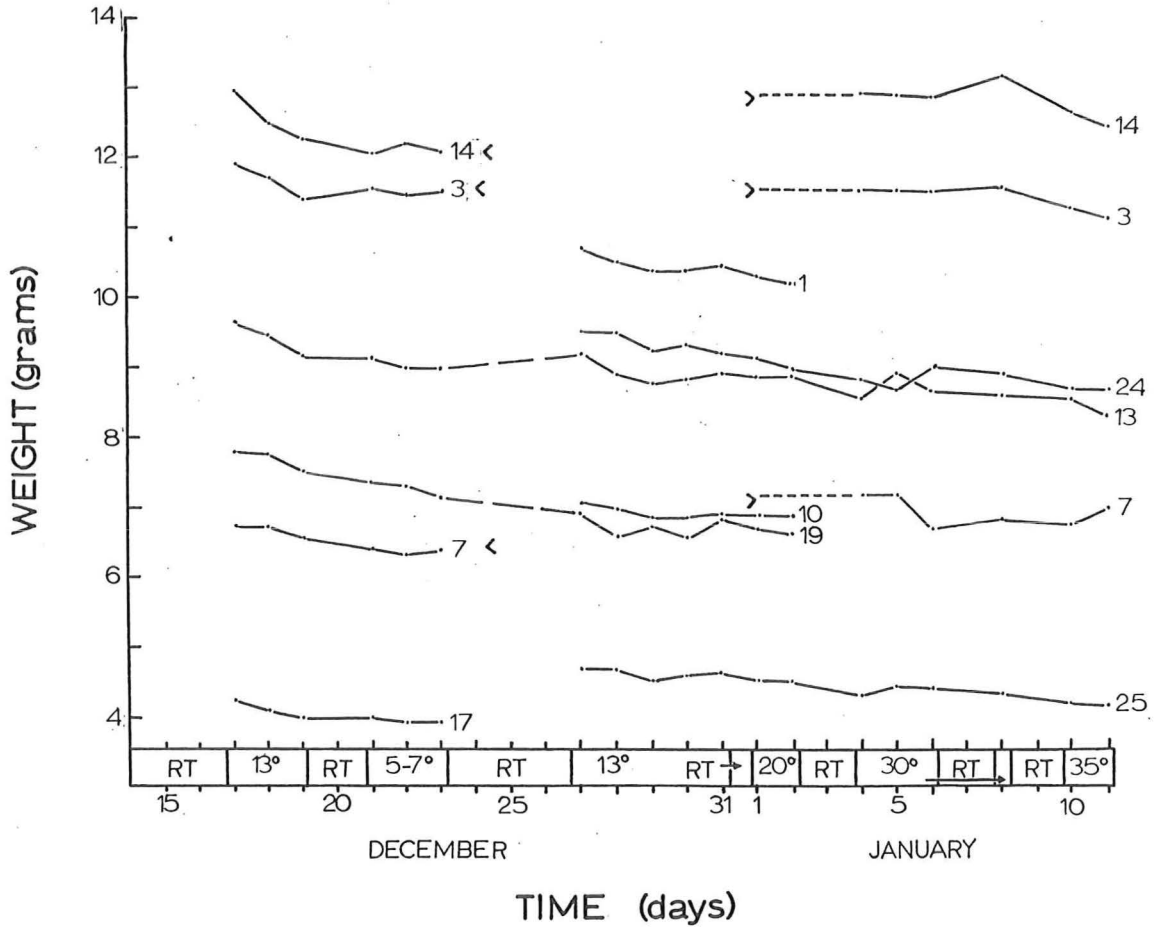

WEIGHT (grams)
14
12
10
8
6
4
14
3
1
24
13
7
10
19
7
17
25
RT
13°
RT
5-7°
RT
13°
RT
20°
RT
30°
RT
RT
35°
15
20
25
31
1
5
10
DECEMBER
JANUARY
TIME (days)

FIGURE 24

Body weights of ten skinks used six at a time for $O_2$ consumption experiments during the final series of trials. Brackets < > enclose the period during which food was available followed by dashes during three days of fasting. Above the abscissa are the $T_A$ of the subjects during the day. All lizards were kept at room temperature (RT) on day between trials and always during the night.

and the slope corresponds to a $Q_{10}$ of 2.24. Although the skinks were unrestrained during the determinations, they were conspicuously quiescent except for the occasional incidents of skinks raising themselves onto their tails against the side of the flask and apparently looking about. Interestingly enough, these incidents occurred a few times at 5 - 7 °C. Three skinks died during the first series of determinations at 35 °C after about seven hours at that temperature. It is not clear whether these deaths were due to the heat or desiccation but it was probably the latter. The S.M.R. of only one other N. Z. lizard has been reported in the literature (Morris, 1965). The nocturnal gecko Hoplodactylus pacificus is of a similar size and appears to have a similar range of values at 18 °C but not at 28 °C (Figure 25). This gecko is probably physiologically adapted to a lower range of temperatures enabling it to have nocturnal habits in a temperate region.

The S.M.R. at 30 °C for Eumeces, Crotaphytus and Gerrhonotus are similar to Leiolopisma even though the species occupy different habitats and are from different families. But when their data are compared at 5 °C, there is no similarity. L. lineoocellatum has a S.M.R. at least four times larger than the least thermophilic species of the group, Gerrhonotus. Possession of a high S.M.R. at both high and low $T_B$ contributes to increased resistance to the cold but at the expense of reduced heat resistance (eg. Eumeces, Gerrhonotus, and Leiolopisma in contrast to Dipsosaurus and Crotaphytus). The $Q_{10}$ for $O_2$ consumption for eight families and fifteen genera of lizards are summarized in Table VI. The temperature dependence of the metabolism of resting lizards shows considerable interspecific variation. For $T_B$ between 15 and 35 °C, most values fall between 1.5 and 3.0. There does appear to be a trend to lower $Q_{10}$ values over the entire range 5 - 35 °C as the species become less thermophilic. Some species appear to have relatively constant $Q_{10}$ over the entire $T_B$ range including the heat resistant

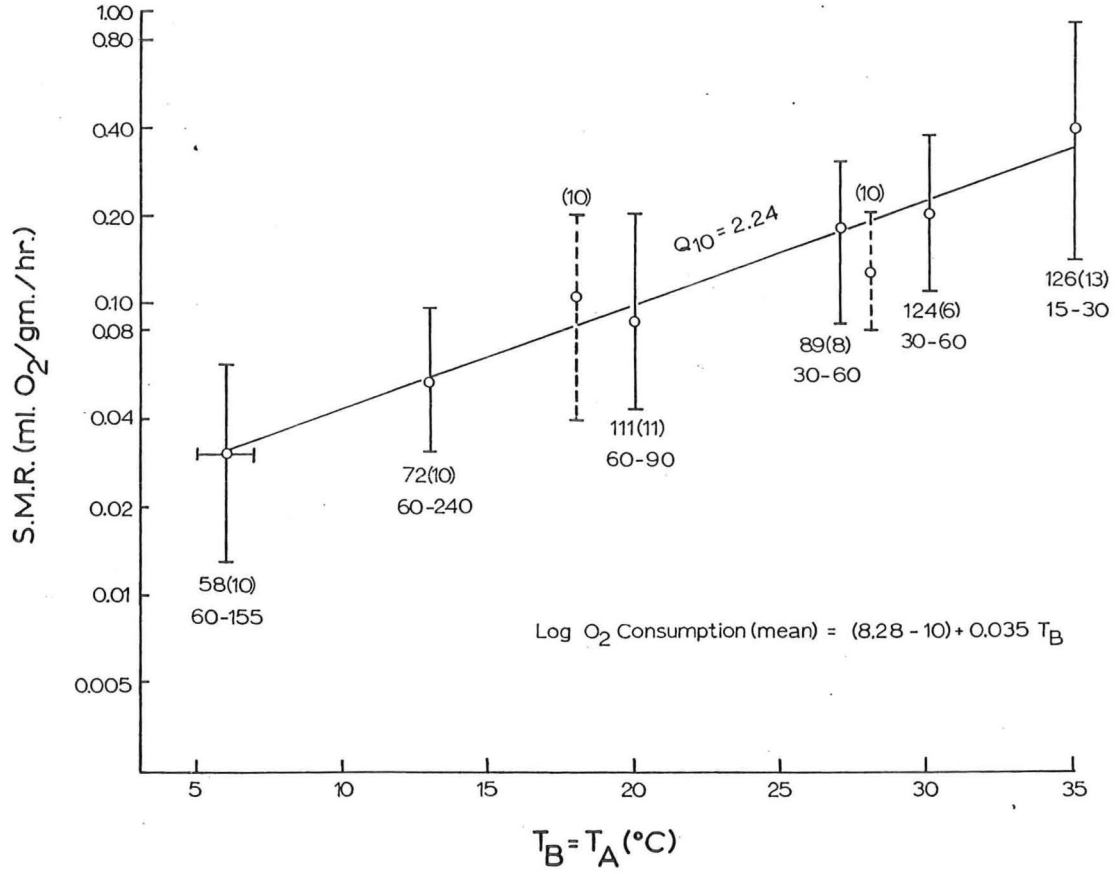

1.00
0.80
0.40
0.20
0.10
0.08
0.04
0.02
0.01
0.005
S.M.R. (ml. O2/gm./hr.)
5
10
15
20
25
30
35
TB = TA (°C)
Q10 = 2.24
58(10)
60-155
72(10)
60-240
(10)
111(11)
60-90
(10)
89(8)
30-60
124(6)
30-60
126(13)
15-30
Log O2 Consumption (mean) = (8.28 - 10) + 0.035 TB

FIGURE 25

Relation of S.M.R. to $T_{EQ}$ at S.T.P. plotted semilogarithmically. Open circles indicate means, vertical lines give the ranges of values. The numerical code gives the number of determinations, numbers of skinks in parentheses, and durations of determinations in minutes. The horizontal line indicates a range of $T_A$. The equation is for the line fitted by eye. For comparison, the range of values for Hoplodactylus pacificus determined by Morris (1965) are included as the dashed vertical lines with the number of subjects in parentheses.

TABLE VI : Temperature coefficients for oxygen consumption of various resting lizards.

| Species and Families | $T_B$ Ranges | | | | | *References |
|---|---|---|---|---|---|---|
| | 5 - 10 | 10 - 15 | 15 - 20 | 20 - 25 | 25 - 35 | |
| Dipsosaurus dorsalis, iguanid | 3.4 | 3.4 | 3.2 | 3.1-2.5 | 2.5 | 12, 17 |
| Cnemidophorus tigris, teiid | 3.6 | 3.6 | 3.6 | 3.6 | 3.6-0.8 | 12 |
| Uma notata, iguanid | 5.4 | 5.4-3.2 | 3.2-1.7 | 1.7-1.4 | 1.4 | 12 |
| Crotaphytus collaris, iguanid | 7.7-6.4 | 6.4-5.7 | 5.7-2.8 | 2.8-2.0 | 2.0-1.7 | 18 |
| Uta stanburiana, iguanid | | 2.5 | 2.5 | 2.5 | 2.5-1.6 | 16 |
| Iguana iguana, iguanid | | | 2.2 | 2.2 | 2.2 | 32 |
| Varanus spp., varanid | | | | 3.3 | 3.3 | 3 |
| Amphibolurus barbatus, agamid | | | 5.6-2.0 | 2.0 | 2.0 | 2 |
| Eumeces obsoletus, scincid | | | | 2.9 | 2.9 | 14 |
| Sceloporus occidentalis, iguanid | | | | 2.4 | 2.4-1.5 | 16 |
| Tiliqua scincoides, scincid | | | | 2.6 | 2.6 | 4 |
| Coleonyx variegatus, gekkonid | 2.9 | 2.9 | 2.9 | 2.9 | 2.9 | 12 |
| Leiolopisma lineoocellatum | 2.2 | 2.2 | 2.2 | 2.2 | 2.2 | |
| Xantusia vigilis, xantusid | 3.2 | 3.2-2.9 | 2.9 | 2.7 | 2.7-1.8 | 12 |
| Gerrhonotus multicarinatus, anguid | 3.1 | 3.1 | 3.1 | 3.1 | 3.1 | 15 |

Note: The species are approximately in order of decreasing thermophily (after Dawson, 1967).

* The numbers refer to entries in the Reference section.

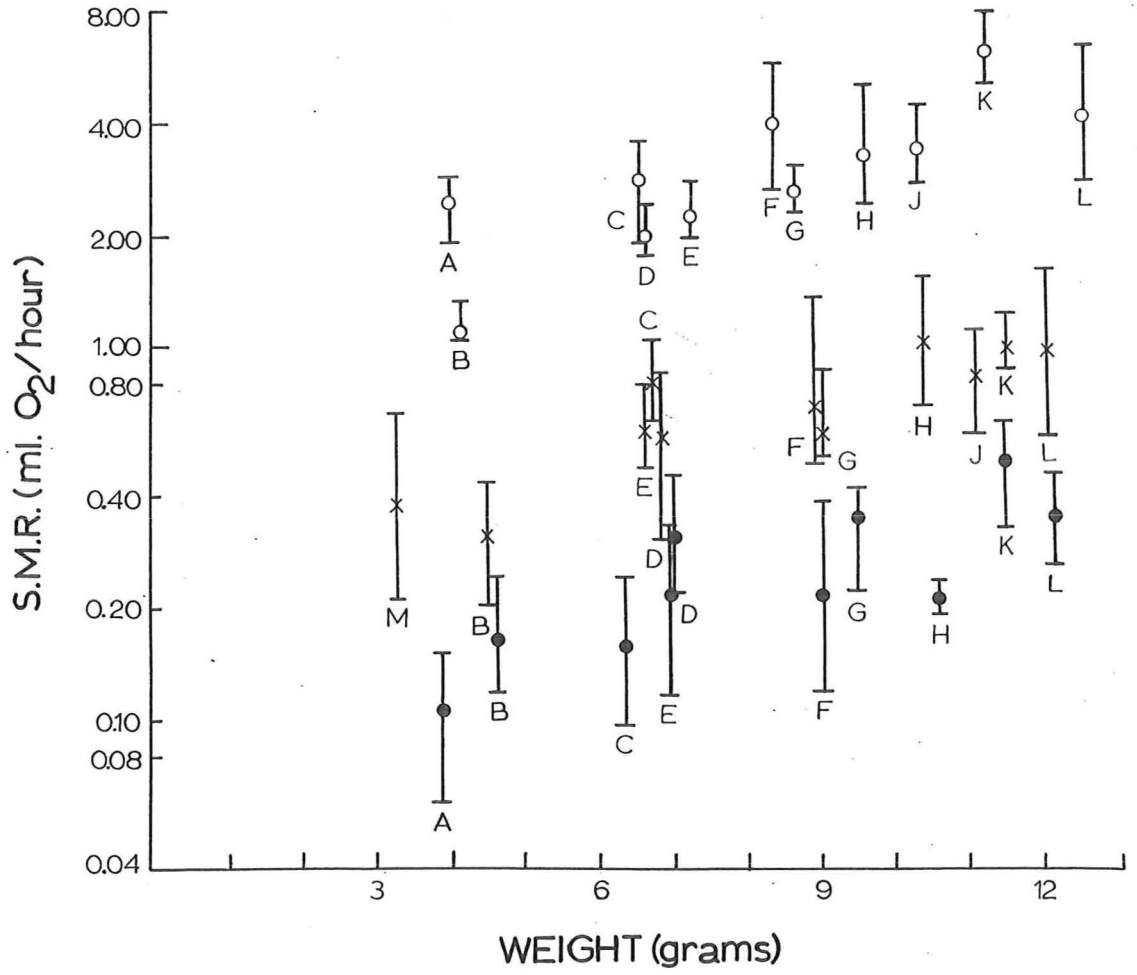

8.00
4.00
2.00
1.00
0.80
0.40
0.20
0.10
0.08
0.04
S.M.R. (ml. O2/hour)
3
6
9
12
WEIGHT (grams)

FIGURE 26

Relation of S.M.R. to body weight plotted semilogarithmically at 35 °, 20 ° and 6 °C (top to bottom) for 12 animals. Means and ranges plotted at average weight during determinations at a particular $T_B$. Capital letters refer to the same animal at different $T_B$. Note that overlap of the S.M.R. occurs between 6 and 20 °C for B and D.

Cnemidophorus and the much less heat resistant forms Coleonyx, Gerrhonotus and Leiolopisma. In other species, the $Q_{10}$ (hence, the slope of the metabolic rate-temperature curve) decreases with increasing $T_B$ (Dipsosaurus, Uma, and Crotaphytus and the less heat resistant Xantusia). It is not known why this variation in S.M.R. to $T_B$ occurs, nor could the different methods employed to measure the rates be entirely responsible since most of the studies have been conducted using the same procedure (Cook, 1949, Dawson and Bartholomew, 1959, Dawson, 1960, Dawson and Tucker, 1963, Bartholomew and Tucker, 1963, 1964, and Bartholomew, Tucker and Lee, 1965). Physiological adaptations of the cardiovascular system, cellular metabolism, or ecological factors may be involved. More information will be needed before a meaningful relationship can be determined for the shape of the S.M.R.-$T_B$ curves and the thermal relations of the species involved.

It is well known that metabolism varies with the weight of an organism. At a given $T_B$, the S.M.R. in millilitres $O_2$/hour of resting lizards varies with the fractional exponent of body weight at both the intra- and interspecific levels. When this S.M.R. is plotted against the weight, there is a general trend at all $T_B$ toward an increase in the rate with an increase in weight (Figure 26 and 27). A four-fold increase in the weight corresponds to about a comparable increase in the S.M.R. Using the data for four families and six genera of lizards, Dawson and Bartholomew (1956) determined an equation for this relationship at 30 °C. Bartholomew and Tucker (1964) revised the equation by including more recent data for five families and eleven genera. There was considerable scatter in the data due, to some extent, to physiological differences among species. The S.M.R. for six skinks (L. lineoocellatum) at 30 °C have been compared to other small lizards and to these lines which were determined for lizards of a wide range of weights (Figure 27). The mean S.M.R. for these skinks are about a half of the predicted values based on the most recent line. The lacertid species had S.M.R. which were on or close to the most recent line. Lygosoma fell well below this line and was

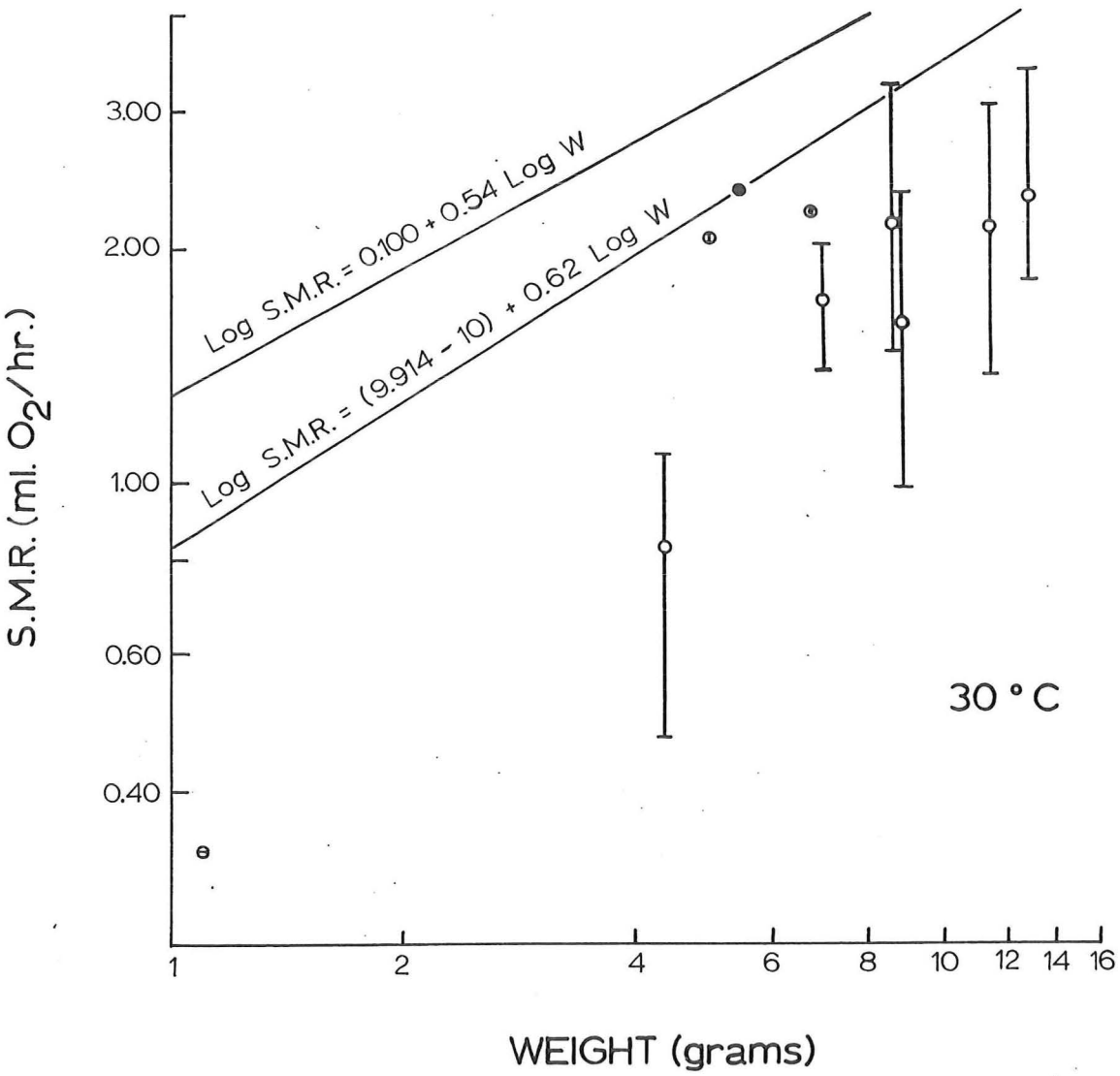

Log S.M.R. = 0.100 + 0.54 Log W
Log S.M.R. = (9.914 - 10) + 0.62 Log W
30 ° C
S.M.R. (ml. O2/hr.)
3.00
2.00
1.00
0.60
0.40
1
2
4
6
8
10
12
14
16
WEIGHT (grams)

FIGURE 27

Relation of Standard Metabolic Rate (ml. $O_2$/hr) to body weight at 30 °C for six animals plotted logarithmically. Ranges (vertical lines) are for 21 determinations. All values were converted to S.T.P. For comparison, the lines and equations determined by Dawson and Bartholomew, 1956 (upper diagonal line) and Bartholomew and Tucker, 1964 are given. In addition, mean values for other lizards are given including ⊖ - *Lygosoma laterale* (Hudson and Bertram, 1966), ● - *Lacerta sicula*, ◐ - *L. muralis*, and ⊙ - *L. melisellensis* (Gelineo and Gelineo, 1955 cited in Bartholomew and Tucker, 1964).

about a quarter of the predicted S.M.R. based on its weight (Hudson and Bertram, 1966). Gerrhonotus, which is over 20 grams, also fell below the line but only by about 25% of the predicted value (Dawson and Templeton, 1966). It may well be that most small lizards are below the line on a log-log graph and that the relationship of the S.M.R.-$T_B$ is curvilinear (particularly for lizards under about 30 grams).

Since all chemical energy derived from specific dynamic action ultimately becomes heat, the measure of the $O_2$ consumed (S.M.R.) determines the endogenous heat production (E.H.P.). For fasted subjects, the oxycalorific equivalent of fat (4.7 calories/ml.$O_2$) is used to convert the S.M.R. to thermodynamic units. This value divided by the dT at 20 °C (that is, 15 °C) gives the thermal conductance due to E.H.P. Using the maximum S.M.R. obtained for any skink at 20 °C (0.20 ml. $O_2$/gm/hr), the thermal conductance due to metabolism would be about 0.06 calories/gm °C hr. This value is about 6% of the mean thermal conductance due to heating or cooling (Figure 17). E.H.P. does not play a very important role in the thermal relations of small ectotherms. The estimate of the E.H.P. of an average sized skink (0.94 cal./gm/hr) would be realistic considering the E.H.P. of similar sized amphibians determined by direct calorimetry at 22 - 26 °C was 0.64 - 0.99 cal./gm/hr (Fromm, 1956). Any E.H.P. would be conducted to the body surface where it would be lost by convection and radiation to the air and by conduction to the ground. Resting terrestrial vertebrate ectotherms could not elevate their $T_B$ (in absence of insolation) above the $T_A$ of the microhabitats available to them. With muscular exercise, however, metabolism increases to the extent that some large ectotherms (and some invertebrates) can temporarily raise their $T_B$ above the $T_A$ endogenously.

Knowing the mean S.M.R. and assuming that a fasting skink is subsisting entirely on its fat reserves, it should be possible to determine the length of time it would take to exhaust these

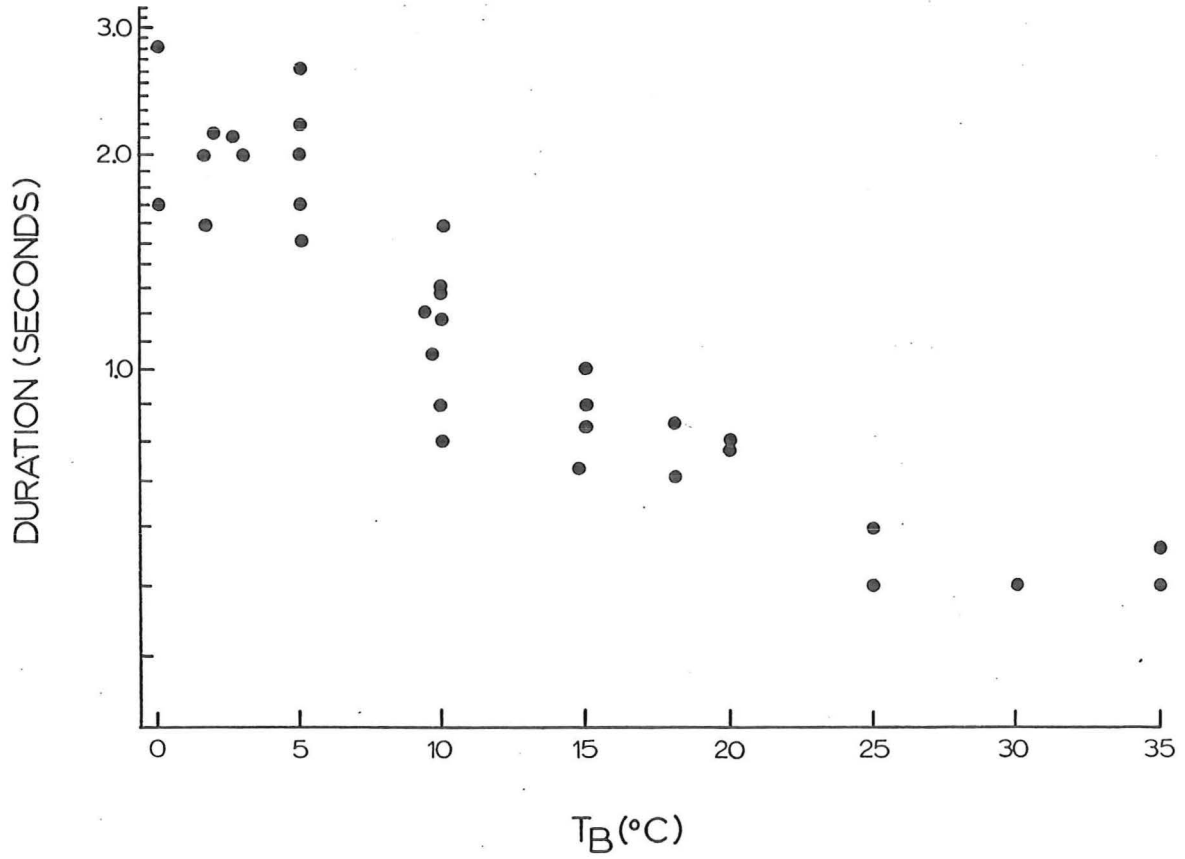

DURATION (SECONDS)
3.0
2.0
1.0
0
5
10
15
20
25
30
35
$T_B$ (°C)

FIGURE 28

Duration of the ~~action potentials~~ electrical activity of thoracic musculature involved in ventilation (EPG) in relation to $T_B$.

reserves. A ten gram skink was found to have two inguinal fat bodies weighing a total of one gram* or 10% of its weight. For the purpose of this calculation, other fat reserves, particularly in the tail, will be disregarded. Assuming that one gram of fat produces 9.5 kilocalories (Prosser and Brown, 1961) and the oxycalorific equivalent of fat is 4.7 cal./ml. $O_2$, the following table gives the theoretical length of time such a skink at a particular $T_B$ could exist, maintaining the status quo. Water would have to be ad libitum.

TABLE VII : The theoretical longevity of a fasting resting skink with fat reserve of 10% of body weight.

| $T_B$ (°C) | 5 | 13 | 20 | 30 | 35+ |
|---|---|---|---|---|---|
| S.M.R. (ml./hr) | 0.2 | 0.4 | 1.0 | 2.0 | 3.4 |
| S.M.R. (cal./hr) | 0.94 | 1.9 | 4.7 | 9.4 | 16 |
| S.M.R. (cal./day) | 22.5 | 47.5 | 112 | 225 | 385 |
| Time (days) | 450 | 200 | 85 | 45 | 25 |

2. Electroorganography

a. Ventilation and Electropneumography (EPG)

Lizards characteristically inhale by drawing their ribs antero-ventrally, an action which is carried out by the intercostal muscles, increasing the volume of the pleural part of thoracic cavity. Since reptiles have no typical diaphragm, the lungs are not completely enclosed in separate pleural compartments. The pattern of ventilation was observed to be the same as for Eumeces (Dawson, 1960) and Lygosoma (Hudson and Bertram, 1966) as well as other lizards. Ventilation is begun with a partial expiration followed immediately by an inspiration (with an

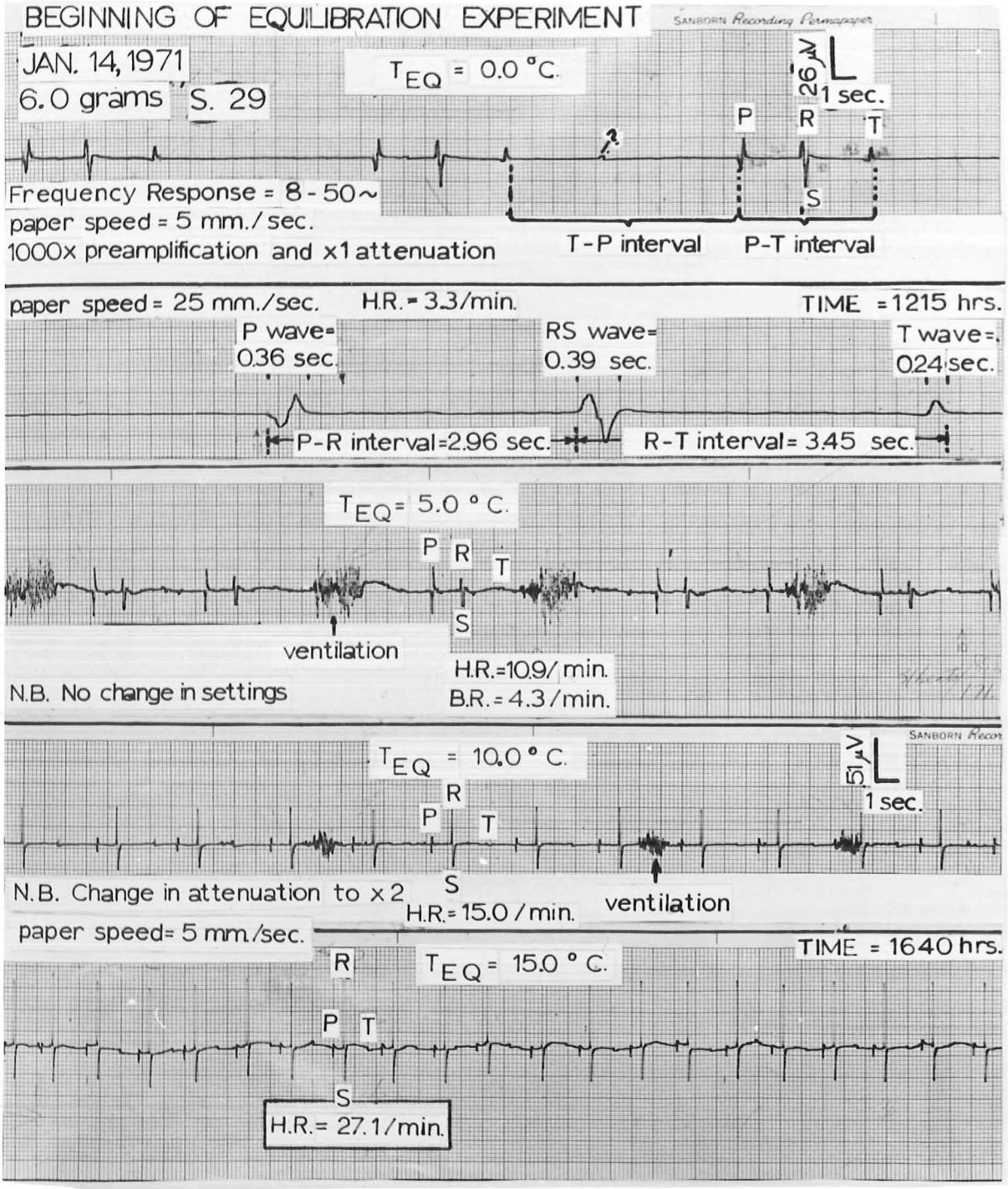
* dehydrated.
+ From data on page 42 indicates that for reasons other than ene these skinks can tolerate only 5-7 hrs. at 35°

expanded thoracic cavity) followed by a partial expiration (passive relaxation of the thoracic musculature). Air is sucked in through the glottis; the sounds of the opening and closing of the glottis are audible at close range.

Typical of most vertebrate ectotherms, the ventilation rate (V.R.) was usually irregular. Since the tidal volume is also variable, the V.R. is not a good measure of external respiration per se. The occurrence of periods of apnoea and the variation in the depth of breathing made it impossible to establish any relationship between the V.R. and $T_B$. The only certain trend was the increase in the incidence of apnoea with a decrease in $T_B$. The rate at 0 $^{o}$C ranged from 0 - 4 breaths during a one minute period (Figure 38, C and J). Apnoea for more than ten minutes was not uncommon and was typically followed by several breaths during one or two minutes. Breathing was so slow and shallow at 0 $^{o}$C that the action potentials of the thoracic musculature (EPG) had to be monitored to confirm their activity. The V.R. at $T_{EQ}$ occurred over a similar range as those obtained during heating and cooling (Figure 19).

Electrophysiological techniques were used to measure the V.R. and the duration during which the thoracic musculature was active (Figure 28). These electropneumograms were the EMG of the intercostal muscles. Templeton and Dawson (1963) determined that the activity of the intercostal muscles was coincident with the duration of the active expiratory and inspiratory events of the ventilation cycle, but not with the partial expiratory action (as the ribs passively return to an equilibrium position). Because the duration of these events was similar to the R-R interval from 20-35 $^{o}$C, EPG were difficult to measure for these $T_B$. At 0, 5, and 10 $^{o}$C, the individual variation in the duration of EPG was about a second. The $Q_{10}$ of the reciprocal of the duration over the range 0-30 $^{o}$C was 2.4.

There was no evidence of panting (voluntary hypernoea) at 35 $^{o}$C. No scincid has been reported to possess this physiological


BEGINNING OF EQUILIBRATION EXPERIMENT
SANBORN Recording Permapaper
JAN. 14, 1971
6.0 grams S. 29
$T_{EQ}$ = 0.0 °C.
26 μV
1 sec.
P
R
T
S
Frequency Response = 8 - 50~
paper speed = 5 mm./sec.
1000x preamplification and x1 attenuation
T-P interval
P-T interval
paper speed = 25 mm./sec.
H.R. = 33/min.
TIME = 1215 hrs.
P wave = 0.36 sec.
RS wave = 0.39 sec.
T wave = 0.24 sec.
P-R interval = 2.96 sec.
R-T interval = 3.45 sec.
$T_{EQ}$ = 5.0 °C.
ventilation
H.R. = 10.9/min.
B.R. = 4.3/min.
N.B. No change in settings
SANBORN Recor
$T_{EQ}$ = 10.0 °C.
51 μV
1 sec.
N.B. Change in attenuation to x 2
H.R. = 15.0/min.
ventilation
paper speed = 5 mm./sec.
TIME = 1640 hrs.
$T_{EQ}$ = 15.0 °C.
H.R. = 27.1/min.

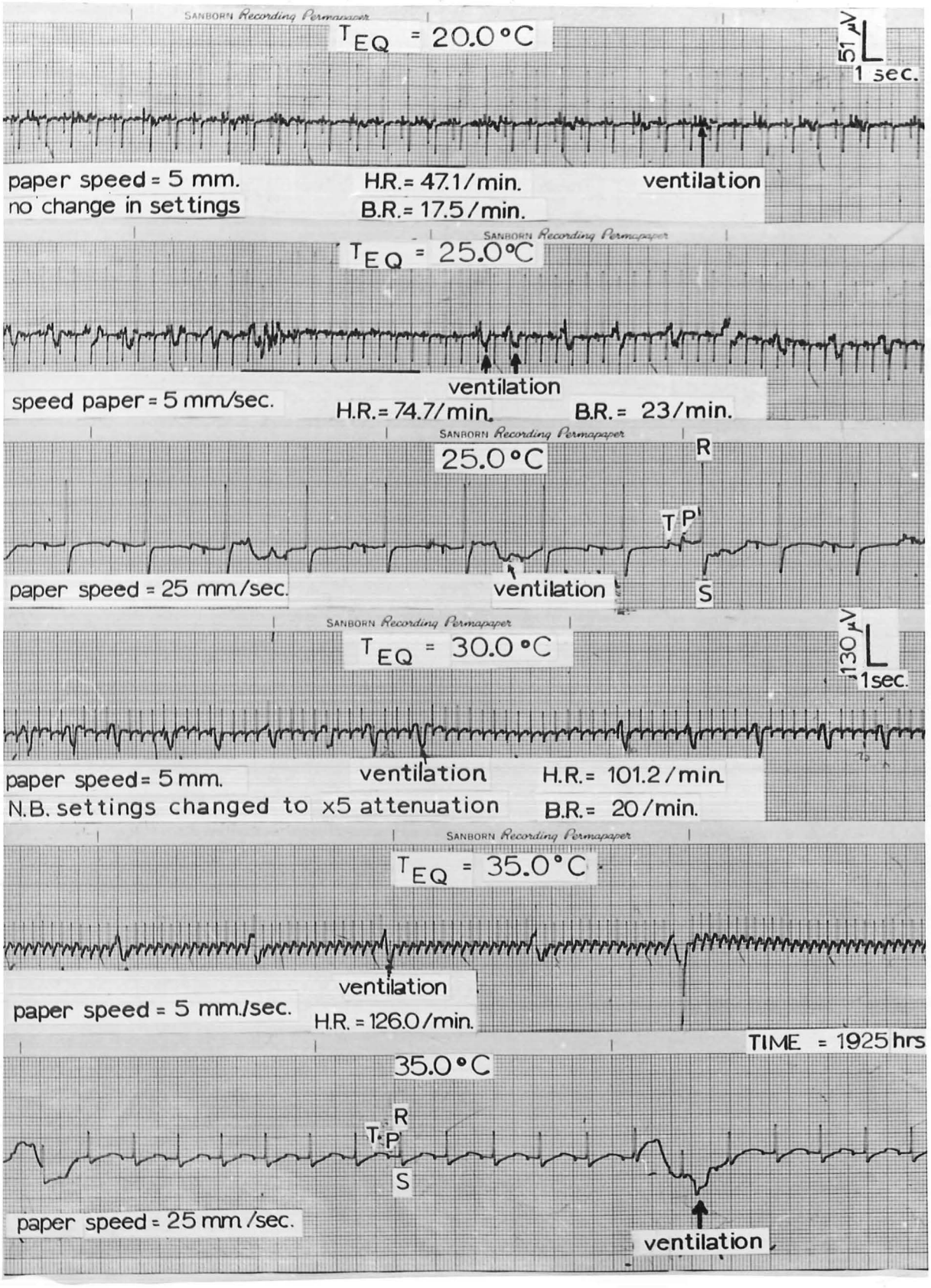

SANBORN Recording Permapaper
$T_{EQ}$ = 20.0 °C
51 μV
1 sec.
paper speed = 5 mm.
no change in settings
H.R. = 47.1/min.
B.R. = 17.5/min.
ventilation
SANBORN Recording Permapaper
$T_{EQ}$ = 25.0°C
ventilation
speed paper = 5 mm/sec.
H.R. = 74.7/min.
B.R. = 23/min.
SANBORN Recording Permapaper
25.0 °C
R
T P
paper speed = 25 mm/sec.
ventilation
S
SANBORN Recording Permapaper
$T_{EQ}$ = 30.0 °C
130 μV
1sec.
paper speed = 5 mm.
N.B. settings changed to x5 attenuation
ventilation
H.R. = 101.2/min.
B.R. = 20/min.
SANBORN Recording Permapaper
$T_{EQ}$ = 35.0 °C
ventilation
paper speed = 5 mm./sec.
H.R. = 126.0/min.
TIME = 1925 hrs
35.0 °C
R
T P
S
paper speed = 25 mm./sec.
ventilation

FIGURE 29

Electroorganograms obtained from one animal at $T_B$ from 0 °C to 35 °C (at 5 degree intervals) from an experiment which took more than eight hours. BR = breathing rate

response to high $T_B$. Eumeces did not pant even at 40 °C, which was well above its eccritic (preferred) $T_B$. The heat resistant iguanids, Dipsosaurus and Crotaphytus, panted above 43 °C, but were immobilized at $T_B$ between 10 and 20 °C.

b. Heart Rates

Electrocardiographic data were obtained from eleven skinks at equilibrated $T_B$ over the range 0-35 °C at five degree intervals. Because of the problem of noise (50 cycle interference and/or EMG), not all the records were interpretable. The recording situations varied daily, and often within the same day, regarding the positioning of grounds, the settings of attenuation and frequency response, and the interference from other electrical equipment in the laboratory and environs. Typical EOG from one subject from an experiment which lasted over eight hours are illustrated in Figure 29. The waveforms changed in appearance among the recordings even though the position of the active electrode was relatively fixed in position (relative to the myocardium). With a 35 degree increase in $T_B$, the heart rates (H.R.) increased from 3.3/min. to 126/min. When these H.R. are plotted semilogarithmically, the $Q_{10}$ for the lines fitted by eye over the ranges 0 - 5 and 5 - 35 °C are 11 and 2.44 respectively. The peak amplitudes of the RS wave at the recording electrodes increased from about 25 to 100 μV. Additional EOG which illustrate other records at 0 °C, or other special features, are presented and explained in Figure 30. When the waveforms on 24 different ECG are analyzed in terms of upward (negative) and downward (positive) deflections, the results are as shown in Figure 31. Using the leads and positions described on page 23, almost all the waveforms are diphasic but 64% were mostly upward or downward deflections (i.e. intermediate between monophasic and diphasic).

There was a linear relation between the H.R. and the $T_B$ for L. lineoocellatum over the range 10 - 35 °C when plotted semi-logarithmically (Figure 32). The equation of the line fitted by eye is

$$\log \text{H.R.} = 1.02 + 0.32\ T_B$$

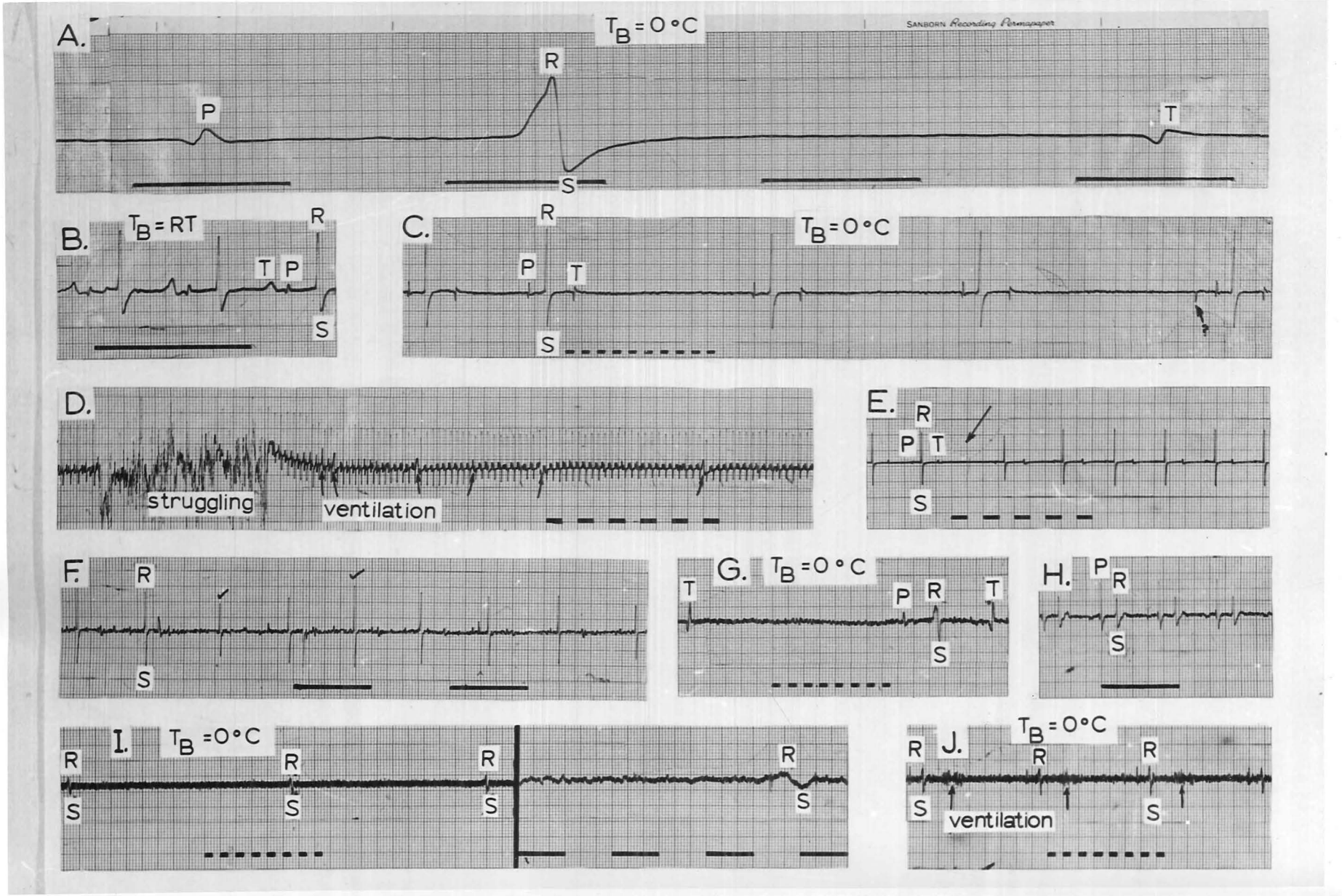

A.
$T_B$ = 0 °C
SANBORN Recording Permapaper
R
P
T
S
B.
$T_B$ = RT
R
T
P
S
C.
R
$T_B$ = 0 °C
P
T
S
D.
struggling
ventilation
E.
R
P
T
S
F.
R
S
G.
$T_B$ = 0 °C
T
P
R
T
S
H.
P
R
S
I.
$T_B$ = 0 °C
R
S
R
S
R
S
R
S
J.
$T_B$ = 0 °C
R
S
R
ventilation
R
S

FIGURE 30

ELECTROORGANOGRAMS

A. An exceptional record at 0 °C for S. 14 where the P wave = 0.28, RS wave = 0.96, T wave = 0.34, P-R interval = 2.08, and R-T interval = 4.28 seconds. Frequency Response = 0.8-50 c.p.s. at X 1000 preamplification and X 5 attenuation. 1 cm. = 130 μV.

B. For comparison, ECG at room $T_A$ at same paper speed as above.

C. Same skink and recording situation at 0 °C but at 2.5 mm./sec. illustrating cardiac arrhythmia (SA block). Although P-T intervals are almost identical in duration, the T-P's are 8.8, 22.2, 20.9 and 25.9 seconds from left to right.

D. EOG of struggling subject during a heating trial. H.R. before was 120.9/min. and after 11 minutes of struggling was 146.1/min. $T_B$ = 32.6 °C.

E. Example of arrhythmia during cooling when $T_B$ = 10.0 °C (S. 10).

F. Modulation of peak amplitudes of RS at 25 °C not apparently associated with ventilation movements. Compare checked waves.

G. ECG at 0 °C with the S greater than the R amplitude and the T is unusually high compared to other waves suggesting that the active electrode was directed slightly caudally (S. 13). X 2 attenuation.

H. Unusually high P wave amplitude at 25 °C (S. 14). The electrode is probably directed slightly rostrally.

I. ECG at 0 °C with noise. Tracings at 2.5 and 25 mm./sec. The noise is largely 50 cycle interference with an amplitude of 2.5 μV. H.R. = 2.25/min. (S. 10).

J. ECG at 0 °C (S. 22) H.R. = 4.2/min. and one breath/heart beat. Noise is about 6 μV, RS = 22 μV. Frequency Response = 0.8-50 c.p.s. and X 1 attenuation.

and its slope corresponds to a $Q_{10}$ of 2.1. Below 10 °C, the relation is curvilinear with the $Q_{10}$ 14 and 4.0 for the ranges 0 - 5 and 5 - 10 °C respectively. The individual variations in the H.R. increased markedly at $T_B$ above 15 °C.

No comparable data for other scincids or even other lizards of similar size are available. The H.R. of some larger resting lizards (of similar weights) obtained with identical methods (Crotaphytus, Dipsosaurus, and Eumeces) showed some differences, suggesting the tenuity of determining a simple H.R.-$T_B$ relation for lizards of different weights. There is, however, a general trend toward an inverse relation of H.R. to body weight for vertebrate ectotherms. The exceptions to this trend are particularly seen at the lower $T_B$. ECG were difficult to obtain in Dipsosaurus below 10 °C and were not detectable at 2.5 °C. Crotaphytus had a significantly lower H.R. at 2.5 °C than Eumeces. Leiolopisma had a similar H.R. to Eumeces (however, only about 1/4 of the P waves were followed by RS waves) at 0 °C, Leiolopisma's H.R. at 5 °C was the same as Eumeces' at 10 °C. This and other evidence shows that Eumeces is not as cold resistant as L. lineoocellatum. Ventricular contractility in Eumeces had a broad peak at 15 - 26 °C. Since it developed a greater proportion of its maximum tension between 10 - 15 °C, it is probable that Leiolopisma would develop its maximum tension at even lower $T_B$, commensurate with its better performance at low $T_B$. An AV block was observed in Eumeces but not in Leiolopisma, further substantiating the claim that the latter species is physiologically adapted to low $T_B$. On the other hand, the suppression of cardiac activity at low $T_B$ for the more thermophilic species seems to emphasize their adaptation to high $T_B$. Since the heart of Dipsosaurus contracted *in vitro* at $T_B$ below those at which ECG were detectable *in vivo*, the implication is that the primary effect of low $T_B$ in suppressing heart action is on the excitability rather than on contractility (Dawson and Bartholomew, 1958).

The $Q_{10}$ are summarized for all lizards reported in the

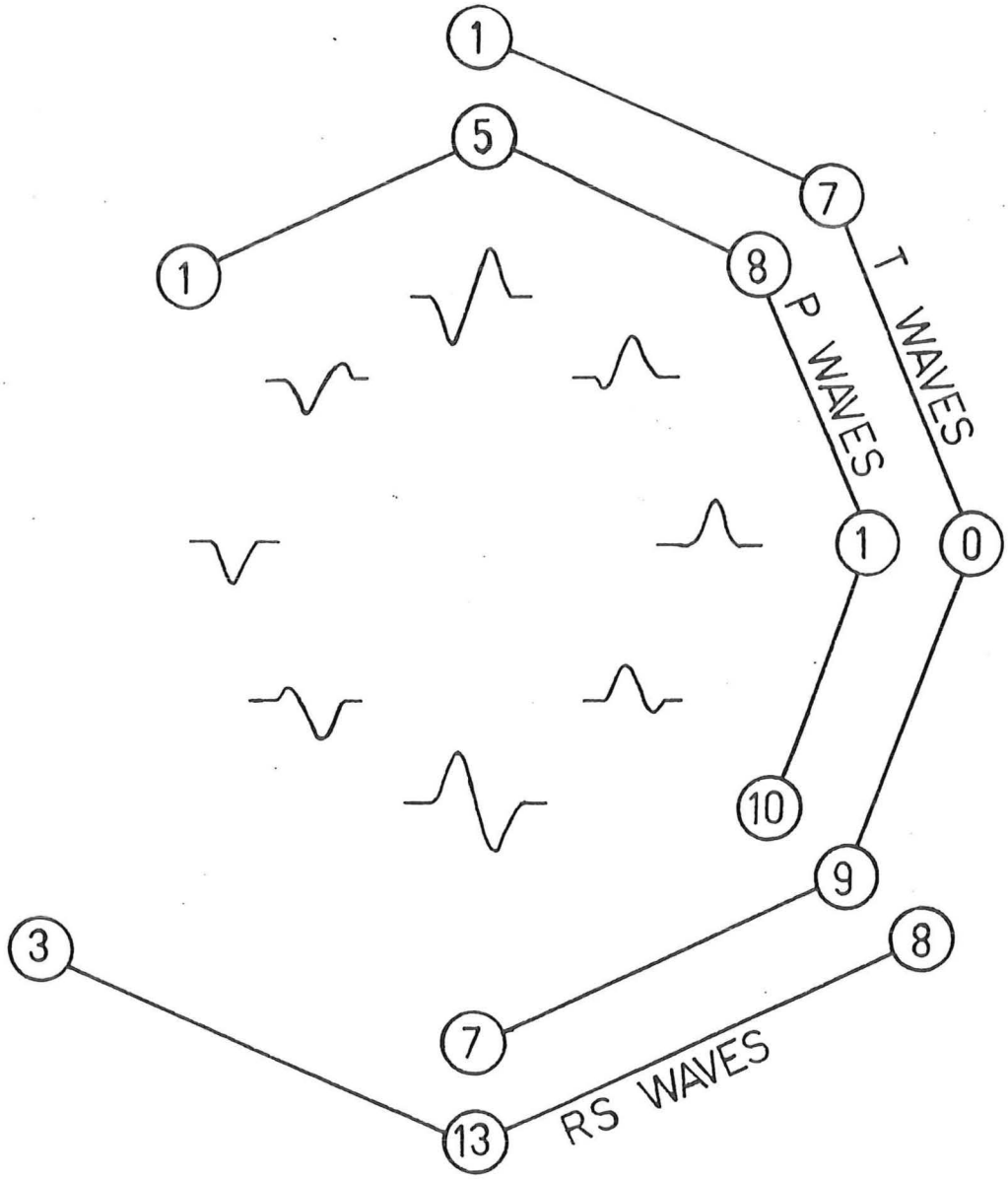

1
5
7
1
8
T WAVES
P WAVES
1
0
10
9
3
8
7
13
RS WAVES

FIGURE 31

Waveforms of P, T and RS waves obtained from 24 different ECG using the leads and positions described in this report. The numbers beside the waveforms indicate the number (out of 24) of ECG that had that form of wave. The numbers for the waves (P, RS and T) are joined for clarity.

literature (six families) on Table VIII. No $Q_{10}$ values for the range 0 - 5 °C have been reported, but several have been determined in the range 5 - 10 °C. The least heat resistant lizards are also the most cold resistant as is to be expected. Above 15 °C, almost all lizards have $Q_{10}$ between 2 and 3. This phenomenon is characteristic of many thermochemical reactions of organisms (van't Hoff's rule). When the $Q_{10}$ values are outside this range, it is generally considered that certain physical processes such as diffusion and conduction are involved. All but Uma are constant between 20 and 35 °C, and there does not appear to be any correlation between the $Q_{10}$ and the thermal relations of the lizard species in this $T_B$ range. The heat resistant lizards are particularly sensitive to $T_B$ below 15 or 20 °C, whereas the more cold resistant lizards show sensitivity below 5 or 10 °C. L. lineoocellatum appears to be one of the more cold resistant forms. An analysis of its cardiac events could possibly elucidate the rate-limiting steps of conduction of the action potentials in the myocardium as detected at the surface of their bodies at low $T_B$.

c. Analysis of the Cardiac Events

A modified version of the Einthoven Lead System was used (Leads II or III) to obtain ECG with bipolar leads - one active and the other indifferent - placed in the manner described on page 23. This method was convenient and successful for obtaining details about the electrical events of the myocardium of L. lineoocellatum.

When the durations of the intervals are plotted semilogarithmically against the $T_B$, the R-T and P-T intervals can be fitted to a line by eye over the entire $T_B$ range studied. The P-R interval can best be described by two lines and has a curvilinear relation to $T_B$. The R-R and T-P intervals show particular sensitivity to $T_B$ below 5 °C (Figures 33 and 34). In fact, the "stretching" of the R-R interval (or the marked decrease in the heart rate) at 0 °C is almost entirely due to the extension of the T-P interval. This also occurred at 15 °C for a cooling experiment (Figure 21). The marked stretching between 0-5 °C was probably due to SA block

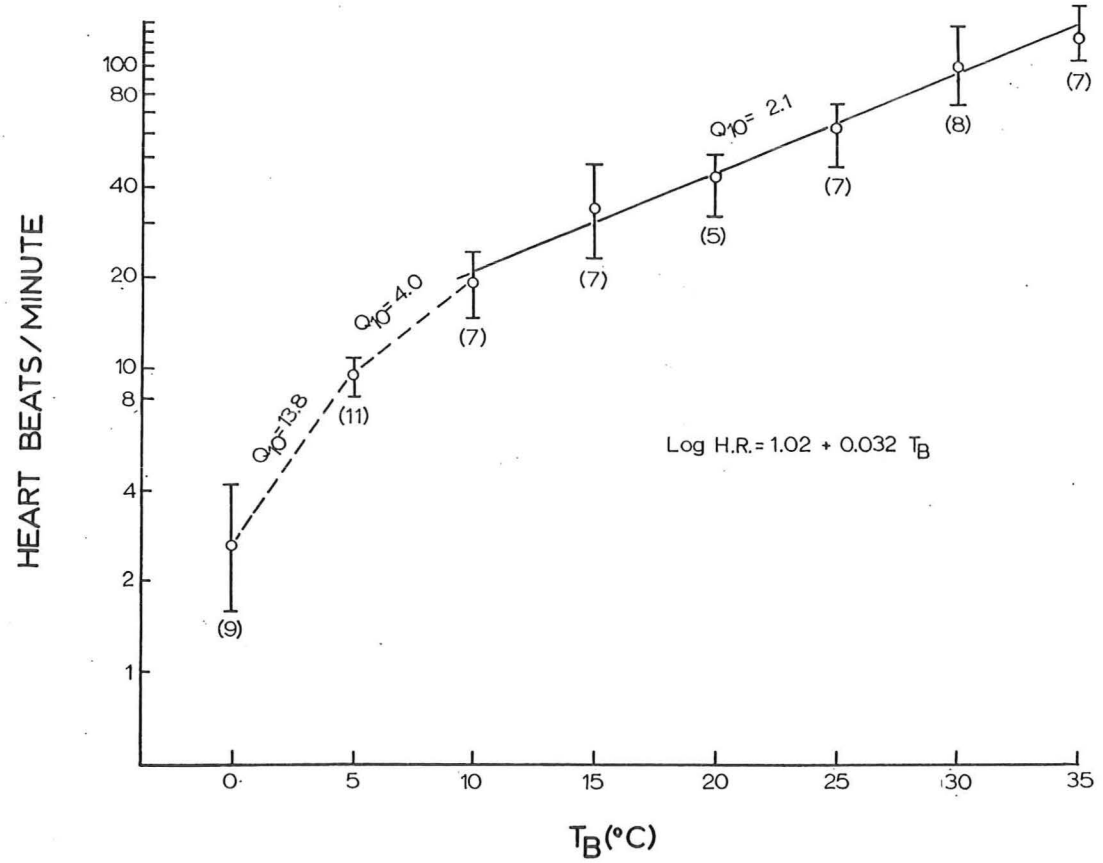

HEART BEATS/MINUTE
100
80
40
20
10
8
4
2
1
0
5
10
15
20
25
30
35
$T_B$(°C)
Q10= 13.8
Q10= 4.0
Q10= 2.1
(9)
(11)
(7)
(7)
(5)
(7)
(8)
(7)
Log H.R.= 1.02 + 0.032 $T_B$

FIGURE 32

Relation of Heart Rate to equilibrated $T_B$. The number of skinks is given in parentheses. The equation is for the line fitted by eye for the range 10 $^{o}$ to 35 $^{o}$C. The vertical lines of this and all subsequent figures are the ranges of values obtained at each $T_B$.

TABLE VIII : Temperature coefficients for heart rates of various resting lizards.

| Species and Family | $T_B$ Ranges | | | | | *References |
|---|---|---|---|---|---|---|
| | 5 - 10 | 10 - 15 | 15 - 20 | 20 - 25 | 25 - 35 | |
| Dipsosaurus dorsalis, iguanid | | 7.2-3.0 | 3.0-2.5 | 2.5 | 2.5 | 12 |
| Uma notata, iguanid | | | | 3.6-3.0 | 3.0-1.8 | 28 |
| Crotaphytus collaris, iguanid | 8.8-5.2 | 5.2-3.1 | 3.1-2.5 | 2.5-2.2 | 2.2-1.9 | 18 |
| Sauromalus obesus, iguanid | 10-3.3 | 3.3-2.8 | 2.8-2.4 | 2.4-2.0 | 2.0 | 41 |
| Amphibolurus inermis, agamid | | | | | 2.5 | 15 |
| Iguana iguana, iguanid | | | 2.0 | 2.0 | 2.0 | 32 |
| Varanus spp., varanid | | | | 2.5 | 2.5 | 3 |
| Amphibolurus barbatus, agamid | | | 3.8-2.3 | 2.3 | 2.3 | 2 |
| Sceloporus graciosus, iguanid | | | 2.4 | 2.4 | 2.4 | 17 |
| Eumeces obsoletus, scincid | 6.5 | 6.5-3.2 | 2.2 | 2.2 | 2.2 | 14 |
| Tiliqua rugosa, scincid | | | | 2.3 | 2.3 | 4 |
| Egernia stokesii, scincid | | | | 2.4 | 2.4 | 15 |
| Leiolopisma lineoocellatum | 4.0 | 2.1 | 2.1 | 2.1 | 2.1 | |
| Gerrhonotus multicarinatus, anguid | 6.9-2.3 | 2.3 | 2.3 | 2.3 | 2.3 | 19 |
| Anguis fragilis, anguid | | 2.3 | 2.3 | 2.3 | 2.3 | 27 |
| Phyllurus milli, gekkonid | | | 1.8 | 1.8 | 1.8-1.4 | 15 |

Note: The species are approximately in order of decreasing thermophily (after Dawson, 1967).

* All the numbers refer to entries in the Reference section.

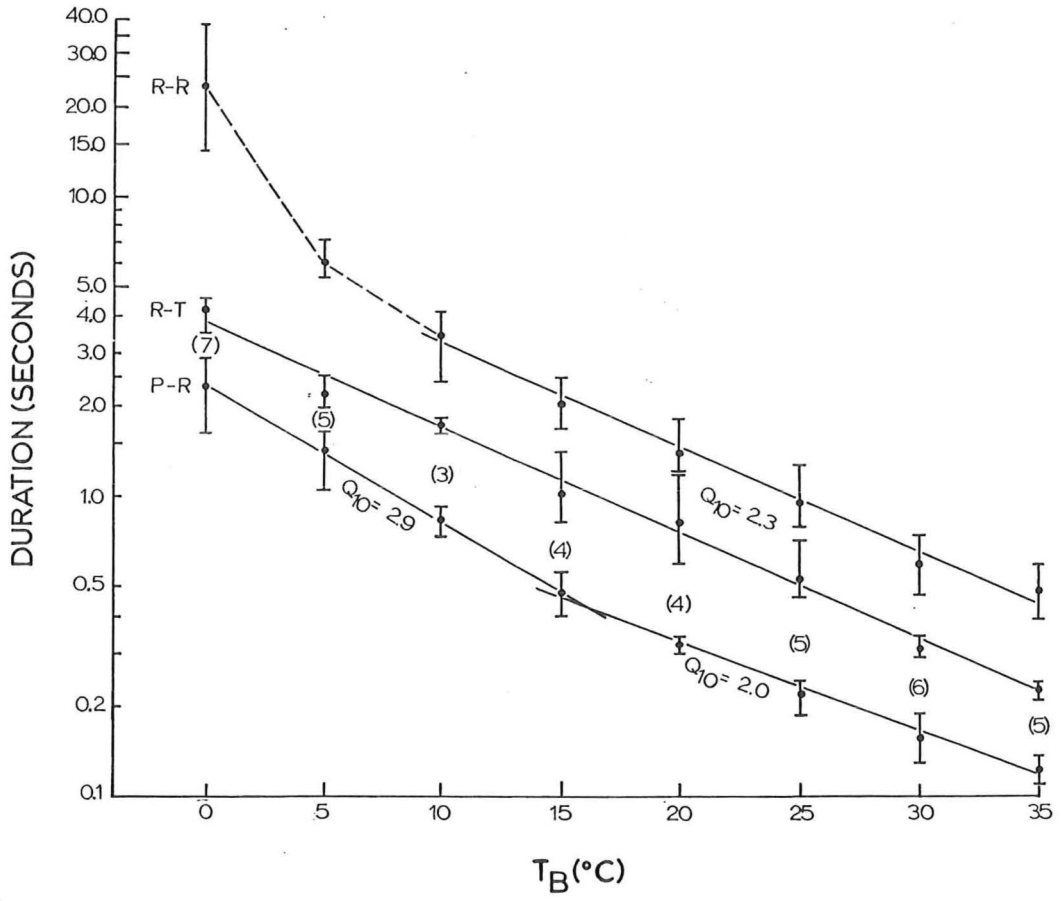

DURATION (SECONDS)
40.0
30.0
20.0
15.0
10.0
5.0
4.0
3.0
2.0
1.0
0.5
0.2
0.1
R-R
R-T
P-R
(7)
(5)
(3)
(4)
(4)
(5)
(6)
(5)
Q10= 2.9
Q10= 2.3
Q10= 2.0
0
5
10
15
20
25
30
35
TB (°C)

FIGURE 33

Duration of P-R, R-T and R-R intervals in relation to $T_B$. Means and ranges of values, and the number of subjects (in parentheses) are given. The R-R interval is the reciprocal of the heart rate (Figure 32). The $Q_{10}$ values are for the reciprocals of the intervals.

or a decrease in the automaticity of the SA node. The $Q_{10}$ of the reciprocals of these intervals are summarized in Table IX.

TABLE IX : Summary of $Q_{10}$ for cardiac events from ECG of *L. lineoocellatum*.

| Reciprocals of events | $T_B$ Ranges | | | |
|---|---|---|---|---|
| | 0 - 5 | 5 - 10 | 10 - 15 | 15 - 35 |
| 1/P wave | 10 | 1.7 | 1.7 | 1.7 |
| 1/RS | 3.8 | 2.0 | 1.5 | 1.5 |
| 1/T | 1.8 | 1.8 | 1.8 | 1.8 |
| 1/R-R interval | 14 | 4.0 | 2.3 | 2.3 |
| 1/P-R | 2.9 | 2.9 | 2.9 | 2.0 |
| 1/R-T | 2.3 | 2.3 | 2.3 | 2.3 |
| 1/P-T | 2.3 | 2.3 | 2.3 | 2.3 |
| 1/T-P | 46 | 3.2 | 3.2 | 3.2 |

When the mean durations of the P, RS and T waves for three skinks are plotted against the $T_B$, the P wave, and to a lesser extent the RS wave show a marked increase in durations at 0 °C (Figure 35). Both these waves involve the depolarization of tissues requiring the physical processes of diffusion and conduction. The T wave is conspicuously less thermolabile at low $T_B$. It is not clear why the repolarization of the ventricle is less affected by low $T_B$ than the reverse process, depolarization. Repolarization is a reparative physiological process which results in the restitution of the membrane potentials and this process requires metabolic energy (Burch and Winsor, 1960). The $Q_{10}$ for the reciprocals of these waves over the range 0-35 °C are summarized in Table IX. The rate of conduction across the auricles is greatly affected by $T_B$ as low as 0 °C whereas the

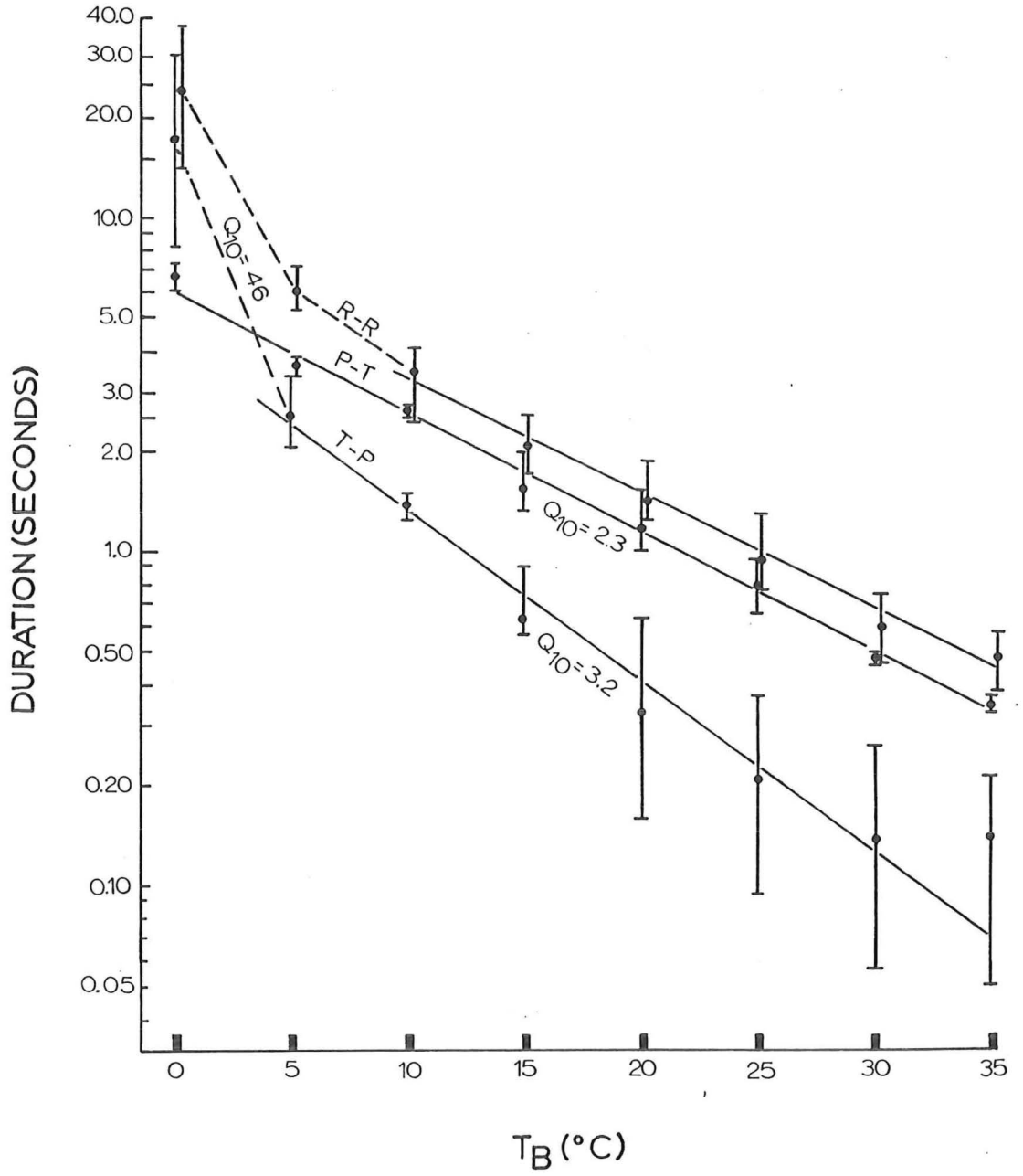

DURATION (SECONDS)
40.0
30.0
20.0
10.0
5.0
3.0
2.0
1.0
0.50
0.20
0.10
0.05
0
5
10
15
20
25
30
35
$T_B$ (°C)
R-R
P-T
T-P
$Q_{10}$= 4.6
$Q_{10}$= 2.3
$Q_{10}$= 3.2

FIGURE 34

Duration of P-T, T-P and R-R intervals in relation to $T_B$. The number of subjects for P-T and T-P intervals same as for P-R and R-T intervals (Figure 33). The $Q_{10}$ values are for the reciprocals of the intervals.

ventricle is only slightly thermolabile. The action of the auricles of Dipsosaurus (in vitro) was suppressed at 9 °C whereas the ventricles ceased to contract at 1.5 °C (Dawson and Bartholomew, 1958).

During the past decade, a large number of saurian ECG have been studied but most have been conducted over the narrow $T_B$ range 20 - 40 °C. Sauromalus, Crotaphytus, and Eumeces are similar to Leiolopisma regarding the $Q_{10}$ of the P-R and S-T (or R-T) intervals over the range 20 - 35 °C. For most of the species studied, the R-T interval has a constant exponential relation to as low as 10 °C whereas the P-R interval has a more complex relation showing a greater sensitivity to low $T_B$. Iguana iguana has a $Q_{10}$ of 1.5 for 1/S-T (15 - 35 °C); $Q_{10}$ of 2.0 for 1/P-R; and $Q_{10}$ of 1.9 for 1/P-T (Moberly, 1968). The durations of these events are about a half of those of L. lineoocellatum at the same $T_B$. Sauromalus has durations which are about twice those of Eumeces, Crotaphytus, and Leiolopisma at the same $T_B$. The increased sensitivity of the P-R interval to $T_B$ below 12.5 °C in Eumeces suggests incipient difficulties in AV conduction since by 2.5 °C, about a quarter of the P waves did not have RS waves following them (AV block). No evidence of AV block occurred on any ECG of Leiolopisma.

The effect of $T_B$ on the intervals and waves of the cardiac cycle has been considered in terms of the durations of these events and their inverse relations ($Q_{10}$). Another method of representing the effect of $T_B$ is to determine the "factor of stretch" for these events. Dawe and Morrison (1955) used this factor (designated K) to characterize the effect of low temperatures on the hearts of hibernating small mammals. They used hedgehogs (Erinaceus europaeus), Arctic ground squirrels (Citellus parryi), and Franklin ground squirrels (C. franklini) since their $T_B$ can drop as low as 0 °C during hibernation. The lowest temperature characteristics of the intact mammalian heart can be known physiologically only for hibernating hearts. These animals maintained their $T_B$ about 2 °C above the $T_A$, so that although they are poikilo-

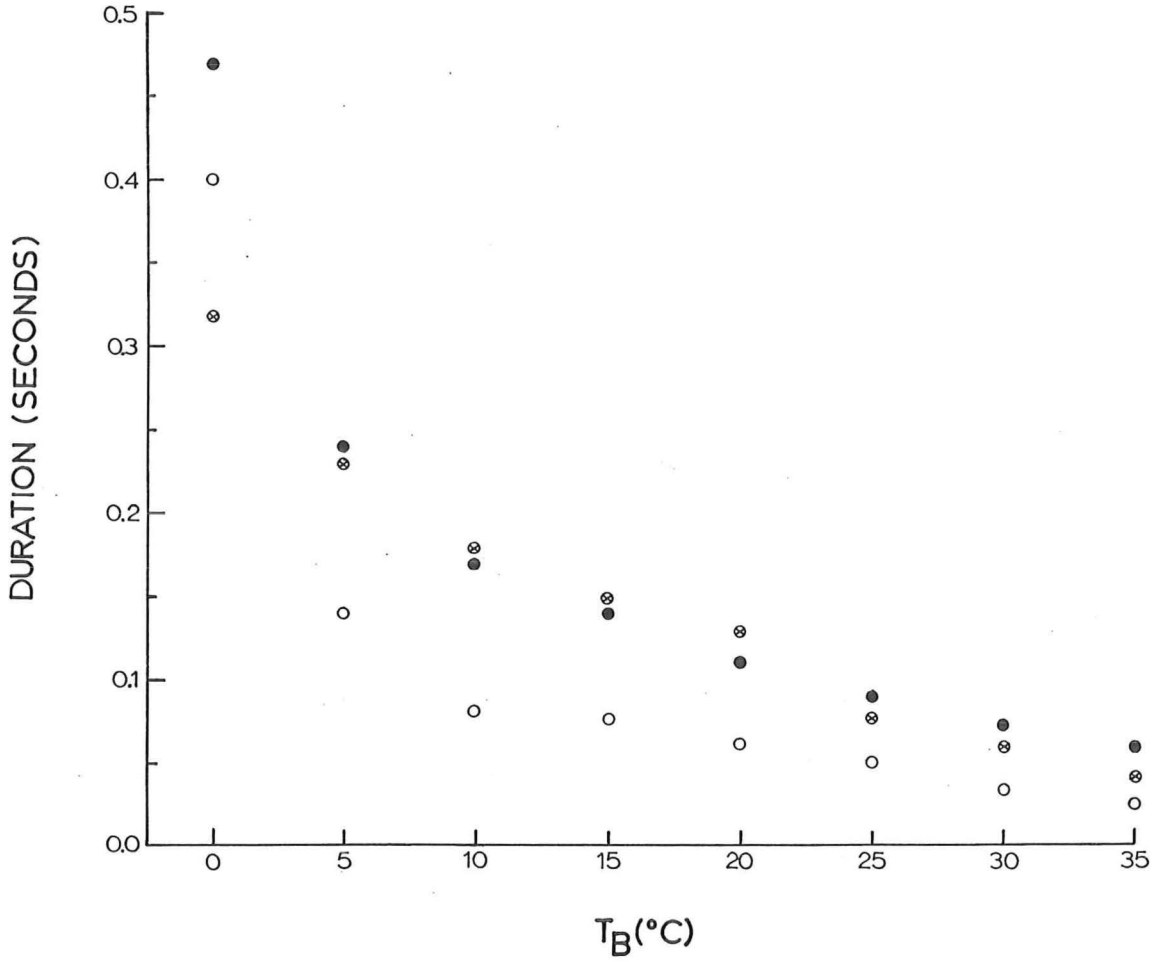

DURATION (SECONDS)
0.5
0.4
0.3
0.2
0.1
0.0
0
5
10
15
20
25
30
35
$T_B$(°C)

FIGURE 35

Mean Durations of $P_9$ $RS_9$ and T waves for three skinks in relation to $T_B$. Symbols are ○ , ● , and ⊗ respectively.

thermic but they are still conspicuously endothermic even during hibernation. Dawe and Morrison's K was defined as follows:

$$K = \frac{\text{duration of cardiac intervals (c.i.) at 0-5 } ^{o}\text{C for hibernating animals}}{\text{duration of c.i. at 33 } ^{o}\text{C for nonhibernating nembutalized animals}}$$

Since L. lineoocellatum has been studied over a similar range of $T_B$ (unlike other lizards in the literature), it is possible to compare the effect of temperature on the hearts of a reptile and a few mammals. For this purpose, two factors will be used, $K_1$ and $K_2$ where,

$$K_1 = \frac{\text{duration of c.i. at 0 } ^{o}\text{C for the skink}}{\text{duration of c.i. at 30 } ^{o}\text{C}}$$

$$K_2 = \frac{\text{duration of c.i. at 5 } ^{o}\text{C for the skink}}{\text{duration of c.i. at 35 } ^{o}\text{C}}$$

Because of the range of $T_B$ and the different species used, the K values are given as a range (Table X). The order of K (from greatest to least) for the mammals was: T-P, P-R, QRS, P, and Q-T. The order for $K_1$ and $K_2$ was the same: T-P, P-R, P-T, R-T, P, T and R.S. The mammalian and reptilian heart appear to be similar regarding the effect of temperature on the T-P and P-R intervals, but the mammalian QRS complex (ventricular depolarization) appears to be more temperature sensitive than the skink RS wave. The reptilian R-T interval is more stretched than the mammalian Q-T. The reptilian P wave is more greatly stretched than for the mammals. These results are revealed when K and $K_1$ are compared. Only the R-T interval of the reptiles is more greatly stretched when K and $K_2$ are compared, and the T-P for the mammals is considerably more stretched. When $K_1$ and $K_2$ are compared, the events showing the greatest to the least foreshortening are: T-P, P, R-T, P-T, RS, P-R, and T.

When the relative durations of certain events are compared with the average duration of the total cardiac cycle (R-R interval),

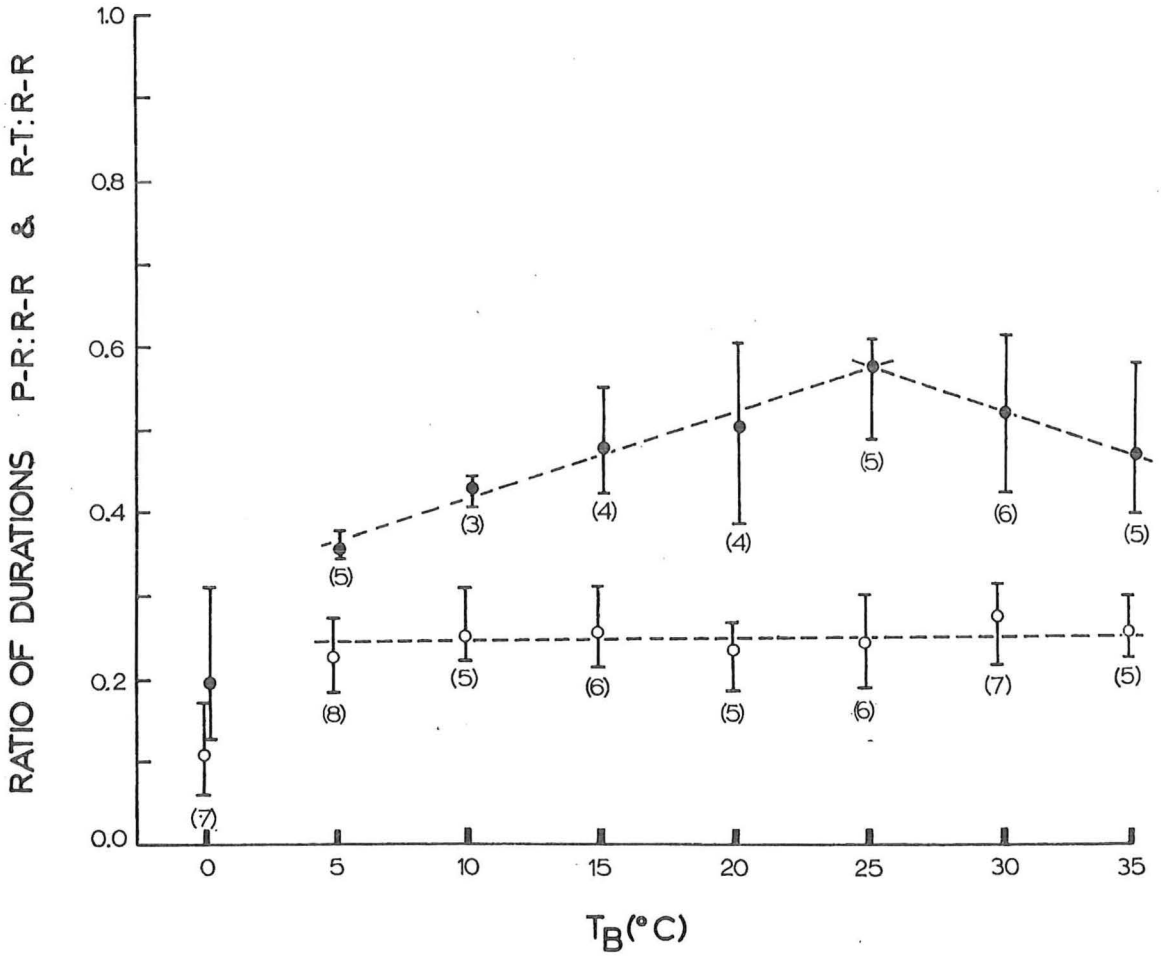

RATIO OF DURATIONS P-R:R-R & R-T:R-R
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
35
$T_B$(°C)
(7)
(5)
(3)
(4)
(4)
(5)
(6)
(5)
(8)
(5)
(6)
(5)
(6)
(7)
(5)

FIGURE 36

Ratios of durations, P-R:R-R and R-T:R-R in relation to $T_B$. Numbers of skinks in parentheses. Symbols are ○ and ● respectively.

TABLE X : Comparison of "factor of stretch" values of L. lineoocellatum with those of the hibernating hearts of mammals.

| Events * | K Range + | $K_1$ | $K_2$ |
|---|---|---|---|
| P-T interval | ---- | 14.0 | 10.3 |
| T-P | 80 - 100 | 128 | 18.4 |
| P-R | 7 - 12 | 14.4 | 12.0 |
| R-T (Q-T) | 4 - 7 | 13.8 | 10.0 |
| RS (QRS) wave | 5 - 9 | 6.4 | 4.0 |
| P | 4 - 8 | 11.8 | 5.6 |
| T | ---- | 7.5 | 5.5 |

* The events in parentheses are the mammalian equivalent.

\+ These ranges were taken off a histogram.

ratios are obtained. When these are determined for each of the $T_B$, the individual contributions of the events are realized. Figures 36 and 37 illustrate these relative contributions. The P-R interval occupies about the same proportion of the cardiac cycle over the range 5-35 °C. The effect of the T-P interval at 0 °C is obvious. The P-R:R-R is about 0.24 and 0.1 for 5 - 35 and 0 °C respectively. The R-T:R-R has a more complex relation to $T_B$. The mean of this ratio is about 0.2 at 0 °C, then increases from about 0.35 to 0.6 between 5 - 25 °C and decreases to about 0.5. It is not clear whether the apparent peak in the ratio of the time of ventricular activity to the total cycle at 25 °C is a reflection of the small sample size or the effect of the T-P interval at the same $T_B$ (Figure 37). When the P-T:R-R and T-P:R-R are compared, the means are 0.2-0.4 and 0.6-0.8 respectively at 0 °C then for the rest of the $T_B$ range their relative contributions are reversed. The period of electrical activity of the skinks heart takes up about 80% (on the average)

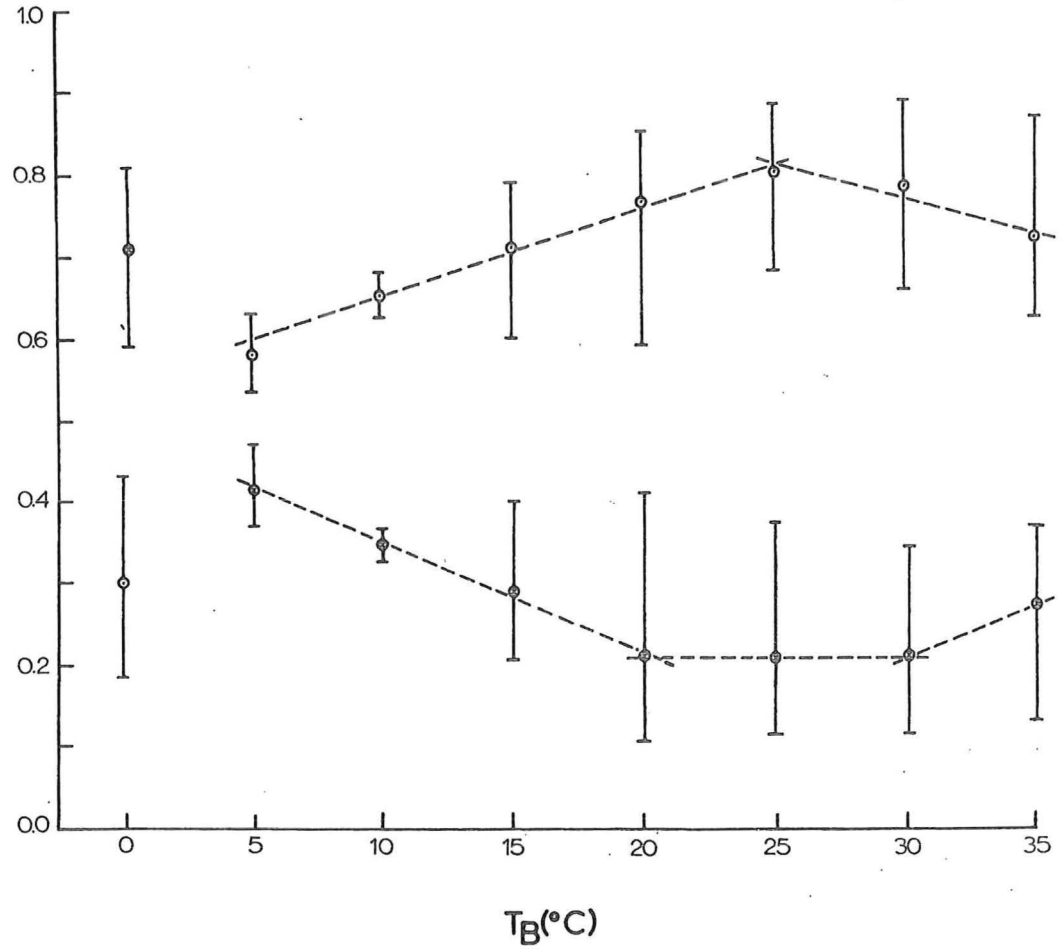

1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
35
$T_B$(°C)

FIGURE 37

Ratios of durations, T-P:R-R and P-T:R-R in relation to $T_B$. Numbers of skinks as in Figure 33. Symbols are ⊗ and ⊙ respectively.

of the total duration of the cardiac cycle at 25 °C. When the P-R:P-T and R-T:P-T are compared, the auricular activity requires 30-40% of the duration of the electrical activity of the skink heart and the ventricular activity takes up the remainder over the entire $T_B$ range. The fact that the R-T is about twice the P-R interval is due to the larger size and the lack of conduction pathways in the ventricle. Mullen (1967) determined ECG for eighteen genera of lizards including only one scincid, Eumeces skiltonianus. The average P-R:R-R and R-T:R-R were 0.29 and 0.61 for the $T_B$ range 22 - 27 °C and they compare favourably with the ratios for Leiolopisma, Mullen (pers. comm.) obtained 0.35 and 0.59 respectively for E. fasciatus (27 °C). These skinks were anaesthetized with pentobarbital. Although their ratios compare well with Leiolopisma, their heart rates and events were about half the values obtained for Leiolopisma. This is largely a function of their size differences.

The long duration of the P-R and the even longer R-T interval are characteristic of the lower vertebrates. Although the relations of the time course of conduction for these events have not been demonstrated electrophysiologically for reptilian hearts, a few histological factors may possibly account for their long durations. Buchanan (1956) studied the gross and minute anatomy of a related N. Z. skink, L. grande. Since the heart of L. lineoocellatum resembles the heart of L. grande in its gross anatomy, it is reasonable to assume that their myocardial tissues are similarly structured. He found that the leiolopismid heart lacks specialized or Purkinje tissue. This fact could be responsible for the delay in the progress of the electrical impulse across the AV junction. The AV junction was found to be complicated by the funnel-like invagination of both atria into the ventricle. The muscle fibres of the AV funnel run caudally and largely circularly, and may, like the AV ring of mammalian hearts, cause the delay in conduction across the AV junction. These factors could account for

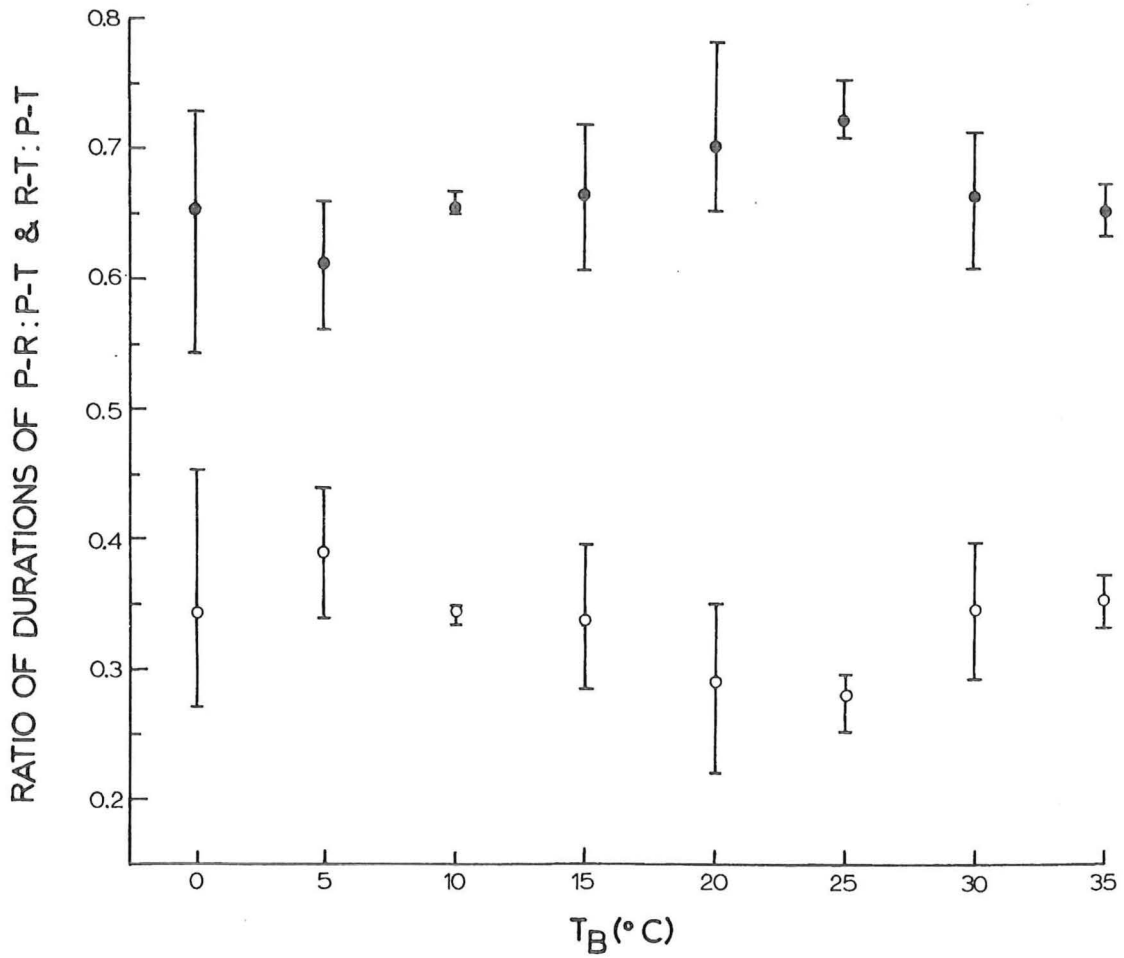

RATIO OF DURATIONS OF P-R : P-T & R-T : P-T
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0
5
10
15
20
25
30
35
$T_B$ (° C)

FIGURE 38

Ratios of durations P-R:P-T and R-T:P-T in relation to $T_B$.
Symbols ○ and ● respectively.

a long P-R interval, but the long R-T interval is much more difficult to account for. If the T wave of reptiles does represent the duration of repolarization of the ventricle, it is not clear why it takes so long for the ventricular fibres to begin repolarization (S-T segment, see Table III). The duration of the T wave did not appear to be particularly sensitive to temperature or to be as stretched as the RS wave (unlike mammals). Augmented vagal tone rather than some intrinsic factor of the ventricle musculature may be responsible.

3. Oxygen ($O_2$) Pulse.

$O_2$ pulse is defined as the $O_2$ consumed/gram/heart beat and is equal to the product of the stroke volume of the heart and the utilization coefficient of $O_2$ (Maynard, 1960).

Although the S.M.R. and the H.R. were not obtained simultaneously, they were obtained under standard conditions so that their mean values at each $T_B$ can be used to determine a mean $O_2$ pulse for Leiolopisma. Table XI shows the $O_2$ pulses which have been determined for lizards. There does not appear to be any correlation between body weight in resting lizards and $O_2$ pulse. It is not known for most species whether an increased $O_2$ pulse is due to cardiac or metabolic responses involving stroke volume or AV difference respectively. In some lizards it increases with $T_B$ indicating that the increased S.M.R. are met by an increased stroke volume and/or the extent to which $O_2$ in arterial blood is utilized. For other species, the $O_2$ pulse remains constant over a wide range of $T_B$ (Iguana) suggesting that an increase in the H.R. is sufficient to meet the increased metabolic demands at higher $T_B$. When the $O_2$ pulse decreases with the rise in H.R., the stroke volume or the AV difference actually decline. These responses do not correlate with the thermal relation of the species nor with their heat resistance. It is not possible to compare the value at 5 $^{o}$C for L. lineoocellatum with other species of lizards. This value is surprisingly high and, based on the theory of $O_2$ pulse, it

TABLE XI : Oxygen pulses of various resting lizards.
(cc $O_2$/gm/heart beat) X $10^{-5}$

| Species | $T_B$ | | | | | | References |
|---|---|---|---|---|---|---|---|
| | 5 | 10 | 15 | 20 | 30 | 35 | |
| Dipsosaurus dorsalis | | | | 3.2 | 3.2 | | 17 |
| Crotaphytus collaris | | 2.4 | | 3.9 | 3.9 | | 18 |
| Sauromalus obesus | | | | 3.5 | 2.8 | | 7 |
| Iguana iguana | | | 3.0 | 3.2 | 3.3 | 3.2 | 44 |
| Varanus spp. | | | 2.8 | 3.1 | 4.2 | 5.0 | 3 |
| Amphibolurus barbatus | | | 3.3 | 4.4 | 3.8 | 3.3 | 2 |
| Eumeces obsoletus | | | | 2.7 | 3.6 | | 14 |
| Tiliqua scincoides | | | | 2.3 | 3.2 | | 4 |
| Leiolopisma lineoocellatum | 5.3 | | *3.3 | 3.4 | 3.4 | 5.2 | |
| Lygosoma laterale | | | | | 4.6 | 3.6 | 25 |
| Gerrhonotus multicarinatus | | 1.8 | | 2.4 | 3.1 | 3.8 | 19 |

Note: The species are approximately in order of decreasing thermophily. (after Dawson, 1967)

* $T_B$ was actually 13 °C.

+ All numbers refer to entries in the Reference section.

suggests that the H.R. has increased sufficiently to meet the metabolic demands and the stroke volume and/or the AV difference has increased substantially at 5 °C. At 35 °C, the $O_2$ pulse again increases markedly suggesting that both factors may have increased.

## GENERAL DISCUSSION

Temperature is certainly one of the most important variables of the physico-chemical environment of organisms, and an important factor in the control of growth of organisms and in their distribution. As a result, considerable study is directed toward an understanding of an organism's thermal relations and thermophysiological responses.

It is an established fact that terrestrial vertebrate ectotherms (T.V.E.) are not simply "die Spielbälle der Umgebung"* but show metabolic adaptations of their protoplasm and exercise behavioural control over their $T_B$. At their eccritic $T_B$, or within their upper range of preferred $T_B$, T.V.E. are as 'warm-blooded' as endotherms and virtually as fast moving, but they are clearly limited in their activity to favourable weather and climates, and to relatively short bursts of activity. Nor are these limitations entirely a disadvantage for a small vertebrate considering the cost of maintaining a $T_B$ endogenously, and the effect on longevity of sustained, intense activity. By preventing metabolic excesses, insuring maintenance of energy reserves and living at a slower pace with relatively long 'resting' periods, lizards are a well adapted and successful group of vertebrates. It is only in very cold climates (arctic), that behavioural and physiological adaptations of T.V.E. prove ineffective; in fact there is nothing they can do to maintain activity (therefore they must avoid freezing and brumate). It is under these conditions that the endotherms have

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* Krehl and Soetbeer, 1899, cited in Bullock, 1955.

the edge on T.V.E. At moderately low temperatures, small T.V.E. are metabolically better off than comparably sized endotherms.

The physiological mechanisms that allow some T.V.E. to move at low $T_B$ have not been investigated. L. lineoocellatum was capable of righting itself in as few as six seconds at 0 $^{o}C$, and of normal locomotion at $T_B$ at least as low as 5 $^{o}C$. On the basis of thermoecological and thermophysiological data, L. lineoocellatum is clearly eurythermic. Eurythermic species are characteristically less sensitive to a wide range of $T_B$ (hence, have relatively lower $Q_{10}$), widely distributed relative to climates, and they tolerate and are active (capable of locomotion) over a wide range of $T_B$ as well as at lower $T_B$. A eurythermic species must also be adapted to reproduce and maintain its population level as well as survive in a 'poikilothermic' and often cold environment. Viviparity is also advantageous for a T.V.E. adapted to low $T_B$. These advantages include increasing mobility of incubation to preserve eggs from direct predation and cold stress; more rapid development since young benefit from mothers' thermal preferences; and resultant increase in mobility of the species for dispersion. There is, however, no clear distinction between oviparity and viviparity. Viviparity ranges from situations in which the eggs are retained as a result of inhibition of the egg-laying responses, to ones in which eggs are formed without shells, to various degrees of placentation, including a situation in which nutrients are transferred to supplement the inadequate yolk (Bellairs, 1969).

Observed interspecific differences in the thermal relations of various species imply that there are physiological adaptations favouring efficiency in physiological performance in particular ranges of $T_B$. Lizards are of particular interest in comparative physiology because they appear to have become adapted to behaviourally established rather than to environmentally imposed $T_B$. This is in contrast to acquatic ectotherms, for example. Also, the organization of T.V.E. is much less dependent on efficient

homeostasis and is generally more tolerant of changes in the milieu interieur. L. lineoocellatum appears to be a very suitable subject for studies involving widely fluctuating and low $T_B$. Since this species is eurythermic, its metabolic processes must be efficient and other physiological adaptations and adjustments must be evidenced over a wide range of $T_B$. Similarly, it would be expected that these conditions would exist at different levels of organization from enzyme systems to intact organisms. This study represents only a preliminary investigation into the thermophysiology of L. lineoocellatum and was limited to the intact organism. The study of its organs and tissues would be rewarding and would be an important step in the understanding of the physiological adaptation at low $T_B$.

Bullock (1955) poses the question of why eurythermic T.V.E. are not more common than they are or why most species are not more widely distributed than they are. He suggests that the limiting factor is an imbalance among various physiological mechanisms so that a morphological or biochemical change is not functionally in proportion to extant processes and therefore is insufficient to be adaptive. This study suggests another approach to the answer. First of all, eurythermic T.V.E. are adapted to low $T_B$. It seems, however, that T.V.E. adapted to high $T_B$ are stenothermal because of the profound physiological adaptations necessary to cope with temperatures higher than those tolerated even by endotherms. Secondly, it is no coincidence that T.V.E. adapted to low $T_B$ are also small in size. Because of the slow rate of heating, large T.V.E. are restricted to the tropics where they tend to be less heliothermic and appear to be sensitive to overheating as well as cooling (alligators die at $4^{\circ}C$) hence they are very stenothermal for a T.V.E. T.V.E. decrease markedly in numbers of species (except for salamanders) as the temperate zone is approached. The diminuition is also observed altitudinally. This is due to the paucity of small viviparous T.V.E. adapted to low $T_B$. Table XII summarizes the reptilian T.V.E. which have been reported to live in cold climates. One species, the tuatara, although active at low $T_B$

TABLE XII : A summary of T. V. E. (reptiles) at low $T_B$.

| Species and Common or Familial Name | Geographical Location Altitude and Latitude | *Reference |
|---|---|---|
| REPTILES - Rhynchocephalia | | |
| Sphenodon punctatum | Islands, Cook Strait, N. Z. 41 °S | 6 |
| Squamata - Saurians | | |
| Hoplodactylus pacificus gecko | Ubiquitous, South Island, N. Z. to 2000 m. 41-44° S | A |
| Leiolopisma zelandica, L. lineoocellatum, L. grande | South Island, N. Z. to 1200 m. 40-44 °S | B |
| Leiolopisma ladacensis | Himalayas 4300 m. 32° N | 31 |
| Leiolopisma pretiosum | Tasmania Mountains above the snowline, 42° S | 21 |
| Lacerta agilis lacertid | Caucacus Mountains 4000 m. 42 °N | 8 |
| Lacerta vivipara lacertid | Eurasia, up to tundra 65 ° N | 5 |
| Liolaemus multiformis iguanid | Andes Mountains, S. Peru 5000 m. 14 ° S | 36 |
| Liolaemus magellanicus iguanid | Tierra del Fuego, S.A. 55 ° S | 5 |
| Phrynocephalus theobaldi agamid | Himalayas 5400 m. 32 ° N | 31 |
| Serpentes | | |
| Thamnophis scalaris garter snake | Mexico 4000 m. 25 ° N | 31 |
| Thamnophis sirtalis garter snake | Eurasia, N. Amer. to tundra 65 ° N | 5 |
| Vipera berus adder | " " | 5 |
| Notechis scutatus poisonous elaphid | Tasmania Mountains above snowline 42 ° S | 31 |
| Agkistrodon himalayanus pit viper | Himalayas 4900 m. 32 ° N | 5 |
| Trimeresurus ammodytoides pit viper | Argentina 50 ° S | 5 |
| Crotalus triseriatus rattle snake | Mexico 4000 m. 25 ° N | 31 |

* All numbers refer to entries in the Reference section.
A. P.M. Johns (pers. comm.) B.A.H. Whitaker (pers. comm.)

at night, is oviparous and probably needs to bask during the day to increase its digestive efficiency. It is, however, severely limited in its distribution because of the slow incubation and the predation of its eggs. Most of the species reported occur on mountains in the temperate zone, rather than near the arctic. It would seem, then, that another reason why T.V.E. species are not more widely distributed is the paucity of small viviparous eurytherms. Leiolopisma species are widely distributed and this is most likely due to their small size, viviparity, and eurythermy.

Small eurythermic T.V.E. are probably best described in terms of their thermophily rather than by their degree of non-heliothermy as Brattstrom (1965) would suggest. 'Facultative nonheliotherm' is not an adequate description of L. lineoocellatum. A better description might be opportunistic or expedient thermophile. When the air and substrate $T_A$ are low, these skinks are probably just as heliothermic as desert lizards adapted to high $T_B$ are. On other occasions, when the substrate $T_A$ are above the skinks' preferred $T_B$ range, their thermotaxic response operates in conjunction with a well developed temperature sense in the selection of the most suitable or advantageous microclimates including making use of filtered insolation or the warm substrate under vegetation (thigmothermic response). As a result of these thermoadjusting activities, eurythermic organisms can achieve a measure of independence from their environmental $T_A$ fluctuations and stresses while being adapted to a wide range of $T_B$.

## SUMMARY

1. The thermal relations, specific heat, heating and cooling rates (thermal conductance), and the physiological responses in terms of metabolic, heart, and ventilation rates to temperature were studied for Leiolopisma lineoocellatum. Electrophysiological techniques were employed to measure the electrical responses of the

intercostal muscles (electropneumography or EPG) and the heart (ECG). The electroorganograms (EOG) were used to determine the rates of ventilation and heart beats respectively, and to provide durations of actual events of specific musculature.

2. Thirty specimens were collected from the Kaitorete Spit ranging from 3.4 to 13.6 grams (average, 8.6 grams) with SVL from 59 to 87 millimetres.

3. The study area, Kaitorete Spit, and the outdoor terrarium were characterized in terms of their thermal relations.

4. Body temperatures ($T_B$) of L. lineoocellatum were measured in a terrarium and in the field under a variety of macroclimatological conditions to determine its thermal relations. The mean $T_B$ of L. lineoocellatum on clear, sunny days in an outdoor terrarium during the period, October 29 to December 1, 1970, was 28.4 $^{o}$C with a maximum of 33.9 $^{o}$C.

5. The specific heat was 0.79 calories/gram/ $^{o}$C (range, 0.74-0.85).

6. The thermal conductance, ventilation and heart rates were determined during heating and cooling experiments. Thermal conductance in calories/gram/ $^{o}$C/hour increased by a factor of about two with a four-fold increase in weight. The times taken for heating and cooling were so rapid that the skinks heated at rates that were the same as or only slightly greater than those at which they cooled. Dead skinks heated and cooled at the same rates. Ventilation rates tended to be lower during cooling than during heating trials. No significant difference occurred between the changes in heart rates during heating and cooling. The rate of heat exchange of small ectotherms is so great that physiological adjustments during heat exchange were considered ineffective.

7. The events of the cardiac cycle during cooling were analyzed and compared to durations of comparable events during equilibration experiments. The effect of cooling on the T-P interval was also noted.

8. The Standard Metabolic Rates (S.M.R.) in ml. $O_2$/gram/hour

were determined over the range 5 - 35 °C. The mean S.M.R. to $T_B$ relation is described by the equation

$$\log O_2 \text{ consumption (mean)} = (8.28 - 10) + 0.035\ T_B$$

with the $Q_{10}$ of 2.24 over the entire $T_B$ range studied. The relation of S.M.R. (ml. $O_2$/hr) to weight was determined and was found to have an inverse relation. Some skinks died at 35 °C.

9. The effect of endogenous heat production on the thermo-economy of L. lineoocellatum was considered.

10. The ventilation rate and the duration of activity of the intercostal musculature were measured electrophysiologically. There was no clear relation of ventilation rate to $T_B$ other than that the incidence of apnoea increased with decrease in $T_B$. No panting was observed. The $Q_{10}$ for the reciprocal of the duration of intercostal musculature activity was 2.4 over the range 0-30 °C.

11. Heart rates were determined over the range 0 - 35 °C. The mean heart rate to $T_B$ relation is described by the equation

$$\log \text{heart rate} = 1.02 + 0.032\ T_B$$

with a $Q_{10}$ of 2.1 over the range 10 - 35 °C. The $Q_{10}$ were 14 and 4.0 for the ranges 0 - 5 and 5 - 10 °C respectively. Individual variation increased markedly above 15 °C.

12. The ECG of L. lineoocellatum were found to contain all the major waves as ECG of mammals. The durations of the intervals and waves were related to $T_B$ in terms of absolute time, reciprocals $(Q_{10})$, ratios of events, and 'factors' of stretch'. The R-T interval was about twice as long as the P-R at all $T_B$. The T-P interval increased markedly between 0 - 5 °C, commensurate with the increase in the R-R interval. The reciprocal of the R-T interval had a $Q_{10}$ of 2.3 over the range 0 - 35 °C, the reciprocal of the P-R was 2.0 - 2.9 over the same range whereas the T-P had a $Q_{10}$ of 3.2 for 5 - 35 °C and 46 for 0 - 5 °C. The durations of the P, T and RS waves also increased with a decrease in $T_B$. The $Q_{10}$ of the reciprocals of these waves were 1.7, 1.8 and 2.0 - 1.5 respectively over the range 5 - 35 °C, and 10, 1.8 and 33.8 over

the range 0 - 5 °C. Based on the 'factor of stretch' values, the temperature sensitivity at 0 °C compared to 30 °C decreased in the order: T-$P_2$, P-$R_2$, R-$T_2$, $P_2$, $T_2$ and RS. These values were compared to those for the hearts of hibernating mammals. No AV block was noted at 0 °C.

13. The oxygen pulse was determined and compared with other lizards reported in the literature.

14. L. lineoocellatum was considered as a eurythermic ectotherm. Terrestrial vertebrate ectotherms at low $T_B$ were discussed. It was suggested that L. lineoocellatum would best be described as an opportunistic or expedient thermophile.

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